





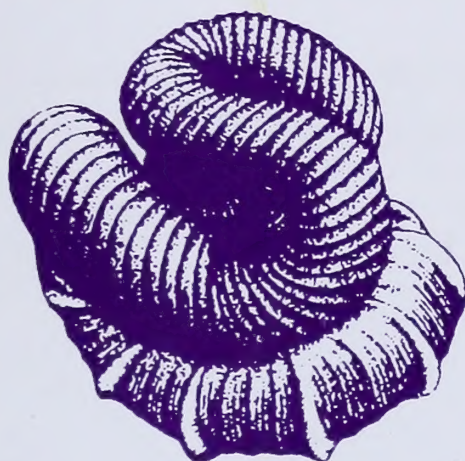


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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nontoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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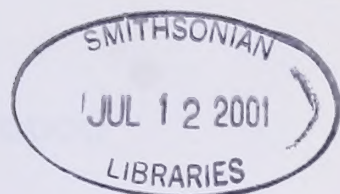
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## Morphological approaches in paleobiology

This special issue is partly based on the workshop of the Palaeontological Society of Japan on "Fossils and Morphology" held at the Misaki Marine Biological Station, University of Tokyo, in Miura City, Japan, from April 21 to 24, 2000. The workshop particularly focused on morphological approaches to paleobiological studies, from both fundamental and practical points of view. Most of the 34 participants of the workshop were young paleontologists interested in morphology.

Research on organic evolution over the Earth's history necessarily depends on the morphology of hard tissues preserved as fossils. Many paleontologists have developed and refined various methodologies for handling the raw morphological data presented by fossils and related extant organisms. However, there has been little reciprocal interaction or feedback in this process. For instance, the skills of an expert in comparative anatomy and the complicated methods handled by a specialist in mathematical morphology are still too far apart from each other. It would seem to be an important goal to make a wide variety of morphological methods accessible to all paleontologists, particularly younger ones.

The workshop setting made it possible to examine the morphological aspects of fossils from a number of viewpoints and provided an opportunity for young paleontologists to learn various methods in morphology. Most major topics concerning morphology, such as functional morphology, constructional morphology, morphometrics, biometry, theoretical genetics, heterochrony, cladistics, comparative anatomy, histology, biomineralization, etc., were covered. Topics included current research on various zoophyla, such as molluscs, arthropods, echinoderms and vertebrates, but there were also abstract discussions of methodology or principle that did not deal with particular groups of organisms. We did not attempt to construct a synthesis of those diverse topics. However, the workshop seems to have succeeded in addressing why so many morphological methods are valuable for paleobiology.

In consequence, the workshop was also a good occasion on which to plan a special issue of *Paleontological Research* on the use of morphology in paleobiology. The present issue partly reflects the activities at the workshop but does not aspire to represent the complete proceedings. The six contributions offered herein cover only a part of the topics presented at Miura. Among the senior authors of this issue, Enrico Savazzi, Takenori Sasaki and Takao Ubukata presented their papers in the workshop, and Richard Reymont and Kazushige Tanabe were welcome additions to the contributors to this special issue. All contributions in this issue underwent the regular review and editing process of the

journal. In addition, several papers which were prepared for this special issue but did not complete the review process in time will be treated as regular submissions.

This collection is diverse, to the extent that perhaps there is no coherent theme. It covers specialized topics such as the morphometrics of ammonites, morphodynamics of an endolithic gastropod, macrosymbiosis in bivalves, early shell morphology of ammonoids, comparative anatomy of gastropods, and the theoretical morphology of bivalve shell structure. Although the papers contained in this issue differ in scope, each touches on the phylogenetic, functional and/or morphogenetic aspects of an organic form. These three aspects may be conceived of as the parameters of a Seilacher's triangle of constructional morphology, in which organic form is postulated to result from the interplay of the three factors. An integrated approach focusing on several aspects of organic form is becoming more and more important as paleobiological researches broaden out to include subjects of evolutionary biology. This issue will serve as a benchmark of the present state of this field and indicate lines of inquiry for future research to follow.

It should be noted that most of the approaches in the papers contained in this special issue were based on handy, "low-tech" methods such as observation or mathematical analysis, and required neither cutting-edge high technology nor the supporting framework of a large project. This collection indicates that morphology based on simple and economical techniques remains an exciting and creative field of science. This fact should encourage the young paleontologist who might feel that his or her work is mere handicraft in comparison to what colleagues who participate in large-scale projects in fashionable high-tech fields are doing. I hope that the topics presented here will be of interest to all paleontologists, and that this special issue will awaken the interest of many students in the field of morphology. I believe that new approaches to morphological studies will play a key role in paleontology in the 21st century.

I thank Tomoki Kase and Kazushige Tanabe, co-editors of *Paleontological Research*, for their help in the course of the editorial process of this issue. Thanks are also due to Rihito Morita for his cooperation in organizing the workshop, to the staff of Misaki Marine Biological Station for their kind hospitality during the workshop, to all participants in the workshop for their active and valuable discussions, and to all of the authors for their thoughtful contributions to this special issue. Although this is only the first time that *Paleontological Research* has collected papers on a specialized theme, I hope it will not be an isolated instance but the first of many to come.

—TAKAO UBUKATA  
JANUARY 15, 2001







## Morphodynamics of an endolithic vermetid gastropod

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**Abstract.** In coiled mollusc shells, the apex typically is located near the centre of a whorl spiral and the aperture at its outer perimeter (exceptions do occur in molluscs with determinate or periodic growth, but they do not invalidate this general principle). This geometry satisfies simple growth and functional requirements. The Recent vermetid *Dendropoma* sp. defies these requirements with its inside-out shell geometry, in which the aperture is located along the axis of the spiral and earlier whorls coil around it. In addition, this species is unique among the Vermetidae in being fully endolithic in the adult, and is one of very few endolithic molluscs with the shell cemented to the substrate during growth. While *Dendropoma* is typically semi-endolithic, several species appear to have secondarily returned to epifaunal coiling as a response to crowding of the substrate. In *D. sp.*, this was prevented by the immediate environment, subjected to a high rate of erosion. This is likely the factor that triggered the onset of endolithic coiling into the substrate. The change from a semi-endolithic to a fully endolithic life habit in this form was probably sudden, since the preadaptations of *Dendropoma* prevent a functioning intermediate stage.

**Key words:** endolithic, evolution, functional morphology, Gastropoda, Mollusca, Vermetidae.

### Introduction

In the adult stage, almost all vermetid gastropods are cemented by the shell to a solid substrate (Morton, 1955, 1965; Keen and Morton, 1960; Keen, 1961; Savazzi, 1996, 1999a, and references therein). As a consequence of this habit, vermetid shells are irregularly coiled or lose all traces of coiling in the adult stage (above references, and below). Most vermetids remove a small amount of material from calcareous substrates before cementing the growing shell margin to it (Savazzi, 1996, and therein). This has the apparent adaptive value of removing superficial layers weakened by encrusting organisms and microborers, and of improving the adhesion between shell and substrate. Observation on free-living gastropods with regularly coiled shells shows that a comparable phenomenon, consisting of a secondary removal of periostracum and a thin outermost layer of shell material, is common at the junction between adjacent whorls. In the latter case, this phenomenon likely enhances adhesion between successive shell whorls. It is reasonable to suppose that removal of the superficial layer of substrate in vermetids may have evolved from the latter, widespread feature (Savazzi, 1996). It is not known in detail how this process is carried out by vermetids, but, as in most instances of secondary shell resorption in molluscs, the process is likely of a chemical, rather than mechanical nature.

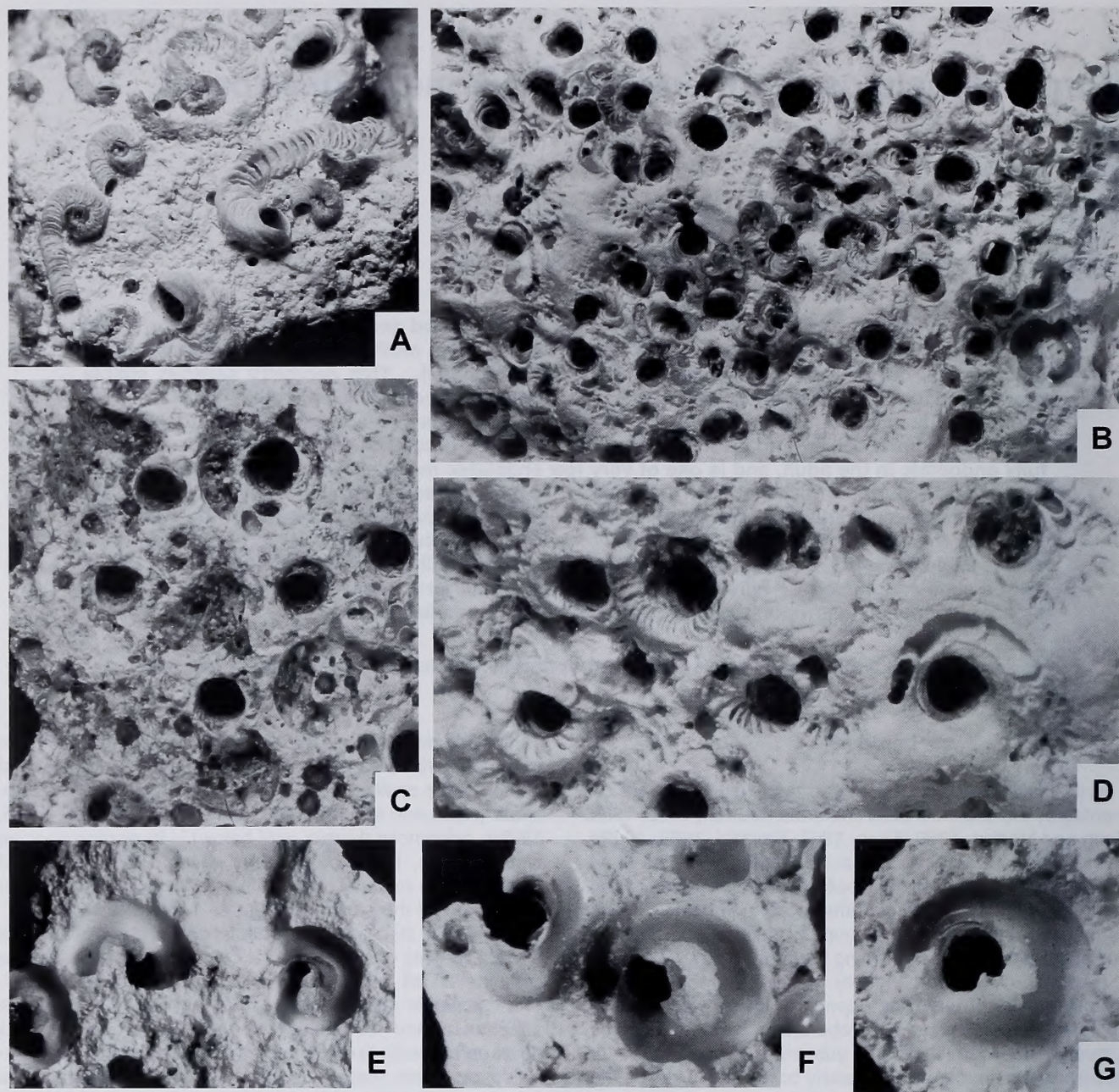
A few vermetids remove a larger amount of substrate, and excavate a trench sunk into the surface of the substrate, into which subsequently they secrete their shells. This trait is

particularly developed in the genus *Dendropoma*, which can be characterised as semi-endolithic because a substantial portion of the shell lies below the original surface of the substrate (Keen and Morton, 1960; Keen, 1961; Savazzi, 1996, 1999a; references therein, and below). In several species of this genus, the shell cavity is covered by a thickened "roof" of shell material, level with or slightly projecting from the surface of the substrate (Figures 1A, 2, and below).

This paper discusses the adaptations and evolution of a Recent species -or ecomorph- of *Dendropoma* with a unique combination of morphologic and ontogenetic characters. The taxonomic position of this form, and whether or not its adaptations and morphology warrant the introduction of a new supraspecific taxon, are discussed summarily, but a decision on these matters is not taken. This organism is hereby referred to as *Dendropoma* sp. because its closest affinities are clearly with this genus. This form differs from typical species of *Dendropoma* in that its adult shell is completely embedded in the substrate, except for the shell opening (see below). This habit can be characterised as fully endolithic, as opposed to the semi-endolithic habit typical of this genus (see above, and below). It is unique among vermetids.

In order to appreciate the unique character of the shell geometry in *Dendropoma* sp., it is useful to review the principal geometric properties of shells that grow by marginal accretion. Coiled mollusc shells typically have the apex located on the axis of a planispiral or helicospiral formed by later whorls. The aperture, on the other hand, is located at the



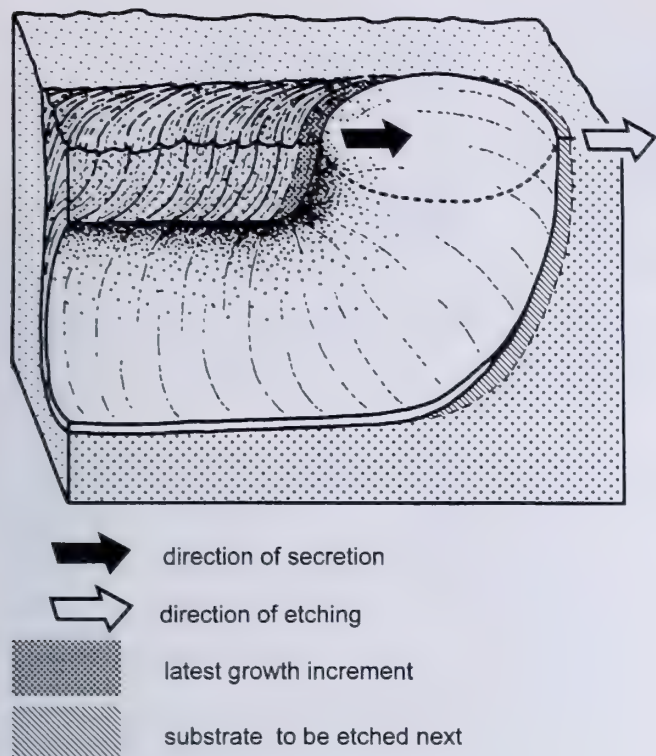


**Figure 1.** A. *Dendropoma annulatum*, Harrington Sound, Bermuda, x 2. B–G. *Dendropoma* sp., Hilotongan Island, the Philippines. Exterior view of substrate (B–D) and view of aperture and internal shell cavity seen from below the surface of the substrate (E–G). B: x 2; C, E: x 4; D, G: x 6.

outer periphery of the spiral. This geometry satisfies simple functional and ontogenetic requirements: it allows continued growth, since earlier shell portions are not in the way of further growth, and yields a relatively compact shell geometry (compatibly with accretionary shell growth). Exceptions to this rule are known, but they do not invalidate the general principle. These exceptions are typically associated with a

“count-down” growth process (Seilacher and Gunji, 1993), in which further shell growth is impossible. This growth process is characterised by “preparatory” morphological changes that precede the attainment of the adult size and the cessation of further growth. For instance, several land snails bring the adult aperture close to the coiling axis in the adult stage, and a few bend the aperture back toward the apex, or





**Figure 2.** Schematic section through apertural region of typical semi-endolithic *Dendropoma*. The surface of the substrate is at the top. The shell cavity has been cut longitudinally through a plane perpendicular to the surface of the substrate and bisecting the shell aperture (the original outline of the aperture is indicated by a dashed line). Note the growth lines on the surface of the shell "roof" and within its structure. Arrows indicate the direction of migration of the aperture along the surface of the substrate during growth, caused by the twin processes of substrate etching (stippled area) and shell secretion (cross-hatched area).

away from it (e.g., Paul, 1999, and references therein). The same principle applies to several heteromorphic ammonoids with count-down shell geometries. A few gastropods (e.g., *Distorsio*), avoid this problem by returning periodically to a more conventional geometry of the last shell whorl, thus allowing the repetition of the count-down process. *Dendropoma* sp., instead, seems to defy the laws of shell geometry and growth by keeping the apertural region of the shell located at the centre of the whorl spiral, and earlier whorls coiled around it (see below) throughout its adult stage, while at the same time extending the length of its shell and increasing its depth within the substrate.

#### Material and methods

The species described in this paper is abundant (Figure 1B) in a band extending from high water mark to about 1 m below it on a rocky shore on the east coast of Hilotongan Island, the Philippines (123° 59' 10"E, 10° 12' 50"N, as measured on Philippine government maps). Population

density exceeds 30,000 adult individuals per m<sup>2</sup> in the densest patches. The surface of the substrate is inclined to the vertical and relatively even. The substrate is a Quaternary, coarse-grained, poorly sorted and somewhat recrystallised biogenic calcirudite, containing occasional large bioclasts (mostly fossil scleractinians). Other areas of this island, as well as most of the nearby islands, were visited repeatedly by the writer, but this species was not observed elsewhere.

Samples of the substrate containing the endolithic vermetid were fixed in dilute buffered formaldehyde and subsequently kept in 5% ethanol. The substrate was bathed in dilute chlorine and mechanically scrubbed to remove adherent algae prior to drying for observation and photography.

#### Morphology and development of *Dendropoma*

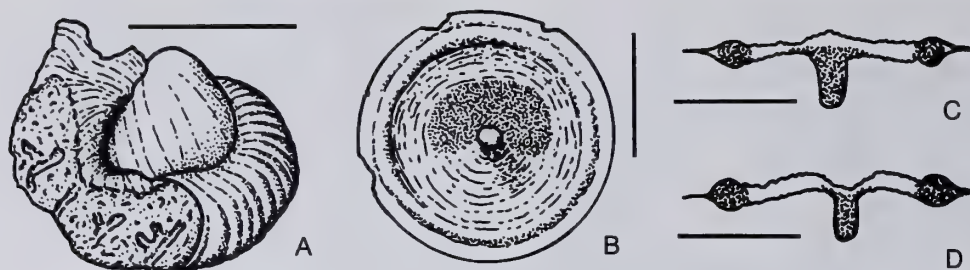
In order to appreciate the affinities of *Dendropoma* sp. with other representatives of this genus, as well as the unique characters of this form, it is necessary to discuss the life habits and morphology of typical *Dendropoma* species.

Sexes are separate. Female individuals of *Dendropoma* house a small number of large embryos within the mantle cavity (Keen, 1960; Hughes, 1978). A veliger stage is absent, and the juvenile passes through a crawling stage before cementing to the substrate. Dispersion of juveniles may be facilitated by wave or current action, aided by the secretion of a mucus thread that retards sinking. However, the sinking rate of juveniles is too high to regard passively transported juveniles as planktonic (Hughes, 1978). Typically, the unattached juvenile shell is trochospiral, brown in colour, and consists of about two whorls.

As in other vermetids (above references), the juvenile shell initially becomes cemented to the substrate by its outer lip. Subsequent shell growth continues along a regular helicospiral trajectory, and lifts the aperture away from the substrate. At this point, the aperture bends toward the apex and reattaches to the substrate by its dorsal region. Shortly afterwards, the mollusc starts partially to sink the shell within the substrate, by eroding the substrate in the region adjacent to the aperture (Savazzi, 1996, 1999a, and references therein).

In adult *Dendropoma* (except for the form in question), two shell geometries and modes of growth are represented. In the first, which is exclusive to this genus, the shell follows an irregular path on the substrate, partly sunk within its surface (Figure 1A; Keen and Morton, 1960; Keen, 1961; Hadfield et al., 1972; Savazzi, 1996). Because of the recessed position of the shell within the substrate, the body whorl is bent outward at an angle of roughly 90° in the region near the aperture, so the plane of the aperture is parallel to the surface of the substrate and perpendicular to the growth direction of the shell (Figures 1A, 2). As a consequence, the aperture moves sideways during growth. Shell secretion takes place along half of the perimeter of the aperture, while erosion of the substrate takes place simultaneously along the other half (Figure 2). The exposed portion of the shell constitutes a "roof" flush with or slightly projecting from the surrounding substrate. Earlier positions of the aperture remain visible as coarse, falcate growth rugae on this roof (Figures 1A, 1C, 3A). The morphology of this relief-pattern is used as a taxo-





**Figure 3.** Juvenile shell showing initial cementation scar (A) and adult operculum in interior view (B) and schematic cross-section (C–D) of *Dendropoma* sp. Scale bars represent .5 mm.

nomic character at the species level. This mode of growth is common among immature individuals of most species of *Dendropoma*, and in the adult stage of solitary species and morphs.

The second mode of growth in this genus consists of piling successive whorls on top of each other, forming an irregularly coiled helicospiral shell. This mode of growth is well represented in other vermetid genera, such as *Serpulorbis*, *Tripsyche* and *Petalococonchus* (e.g., Keen, 1961; Savazzi, 1996, 1999a). In *Dendropoma*, this morphology is frequent in gregarious species and on crowded substrates.

In the adult stage, vermetids exhibit dextral coiling, or no coiling at all (above references). Since the adult shell portion is cemented to the substrate, or to earlier whorls, by its dorsal surface (see above), the whorls coil in the counterclockwise direction when viewed from above. Sharp bends of the shell in a sinistral (i.e., clockwise) direction are uncommon, and vermetids generally do not exhibit the meandering in alternate directions which is frequently seen in cemented serpulid polychaetes. As discussed by Savazzi (1996), sinistral bending in the Vermetidae is probably prevented by the laterally asymmetrical placement of the columellar muscle.

*Dendropoma* possesses a corneous operculum, the morphology of which is used as a species-level taxonomic character (Keen and Morton, 1960; Keen, 1961; Morton, 1965; Hadfield *et al.*, 1972). Common to all species of *Dendropoma* is a secondarily thickened central portion of the operculum, forming an inward projecting boss or elongated "handle" (above references, and below).

Several species of *Dendropoma*, as other vermetids, are gregarious and form exclusive or oligotypic associations in the intertidal and shallow subtidal zones, sometimes building small reefs (Keen and Morton, 1960; Keen, 1961; Kempf and Laborel, 1968; Hadfield *et al.*, 1972; Hughes, 1978, and personal observations).

### Morphology and growth of *Dendropoma* sp.

#### Larval and juvenile development

Females incubate few (from 6 to 12) large eggs within the mantle cavity. Mature embryos contain a well developed protoconch consisting of approximately 2 whorls. This shell is translucent, smooth when observed under a dissection mi-

croscope, and brown-coloured.

Samples of the substrate inhabited by adults of this species were found to harbour numerous juvenile specimens, usually nested in small crevices. As typical of vermetids (above references), juveniles first cement to the substrate by the outer shell lip. Immediately afterwards, the shell bends in the apical direction, usually lifting free of the substrate, and subsequently reattaches to the substrate by the (homologically) adapical surface of the whorl.

The size of the shell in the smallest attached juveniles is comparable to that of the largest larval shells. Therefore, a veliger stage is apparently lacking. This agrees with observations on other species of *Dendropoma* (see above references).

#### Immature shell

At this stage, the shell is light brown to white with occasional brown patches (especially on its interior surface), carries coarse falcate ridges on its exposed surface, and is slightly sunk within the substrate. Except for the rather small size of *D. sp.*, young specimens (central portion of Figure 1B) are essentially identical, in general appearance, to the adult stages of several other species of *Dendropoma* (e.g., Figure 1A).

Some of the individuals of *D. sp.* afterwards continue to wander in an apparently random fashion during growth, perhaps as a response to a crowded or irregular substrate. Most of the individuals, however, after an irregular early stage build an evenly curved, counterclockwise arch (surrounding the adult shell aperture of several individuals in Figure 1D). The radius of this arch, which gradually extends to one full whorl, is rather constant in length among different individuals, and the free space enclosed within the arch has a diameter comparable to that of the adult shell aperture. While building this arch, the apertural region of the shell becomes gradually embedded deeper within the substrate, thanks to a gradual increase in etching activity. Earlier portions of the body whorl do not change their position relative to the substrate.

#### Adult shell

Upon reaching one whole, broadly umbilicate whorl, the apertural portion of the shell, instead of rising onto and overlapping the earlier portion of the whorl as in other vermetids



(see above), dips beneath it and into the substrate. At the same time, the shell aperture bends toward the umbilicus, thus avoiding the erosion of earlier portions of the arch. It is convenient to characterise these events as the beginning of the adult growth stage of the shell, although they may have no connection with reproductive maturity.

From this moment onward, the shell aperture opens within the umbilicus (Figure 1D-G). Further growth continues in the same fashion, with subsequent whorls becoming embedded deeper within the substrate, and the aperture located at the bottom of an umbilical well surrounded by earlier whorls (Figures 1C-G, 5). As a result, the shell is coiled in an apparently sinistral fashion. However, since the shell initially attaches to the substrate by the adapical side of the whorl, this coiling geometry is not sinistral, but hyperstrophic dextral.

Substrate-etching continues to take place within the aperture, which revolves around its axis and moves deeper within the umbilical well. This results in the formation of a pattern of spiralling ridges on the walls of the umbilical well (Figure 1D, bottom of Figure 1C, centre of Figure 5A). These ridges are homologous to the falcate ridges on the exposed surface of the shell in semi-endolithic species of *Dendropoma*. The largest individuals of *D. sp.* display an internal shell cavity consisting of about two whorls. The earliest, most superficial of the preserved shell whorls are commonly eroded (Figure 1C), with the shell cavity exposed and closed off by internal septa (rightmost portion of Figure 1D). Thus, this portion of the shell is gradually vacated and sealed off by the mollusc. In some specimens, judging from the diameter of the shell cavity, at least one or two additional whorls were originally present, and were destroyed by rapid erosion of the substrate. This is further supported by the frequent occurrence of radular scratch marks on the surface of the substrate (probably caused by chitons and archaeogastropods, which are both frequent in crevices and sheltered areas), and by a general lack of cemented epifauna.

### Operculum

The operculum (Figure 3B-D) is corneous, white with reddish-brown periphery and nucleus. It is variable in general shape, with the outer surface slightly concave to highly domed (Figure 3C-D), carrying irregular concentric ridges but no visible spiral ornamentation. The perimeter consists of a thin lamina surrounding a thickened and bulging ring (Figure 3B-D), which, unlike the rest of the outer surface, is smooth and shiny. The inner surface of the operculum is smoother and carries an elongated axial "handle" (Figure 3C-D) and a semicircular or horseshoe-shaped dark patch near the basis of the handle (Figure 3B).

### Soft parts

The general appearance of the body (Figure 4) is consistent with that of other species of *Dendropoma* (above references). The body is rather short, with a well developed columellar muscle. The mantle is slitted in the female, whole in the male. The pedal and cephalic tentacles appear to be rather short. A detailed anatomical investigation was not carried out.

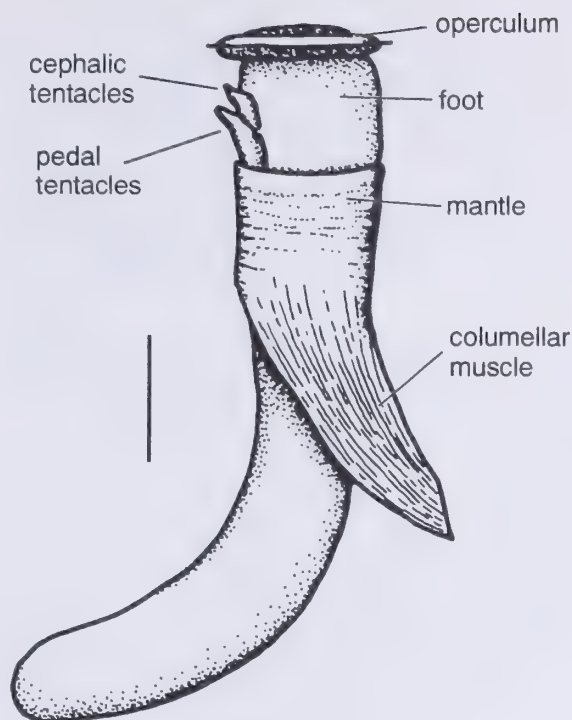


Figure 4. Soft parts and operculum of male *Dendropoma sp.*, in lateral view. Scale bar represents 5 mm.

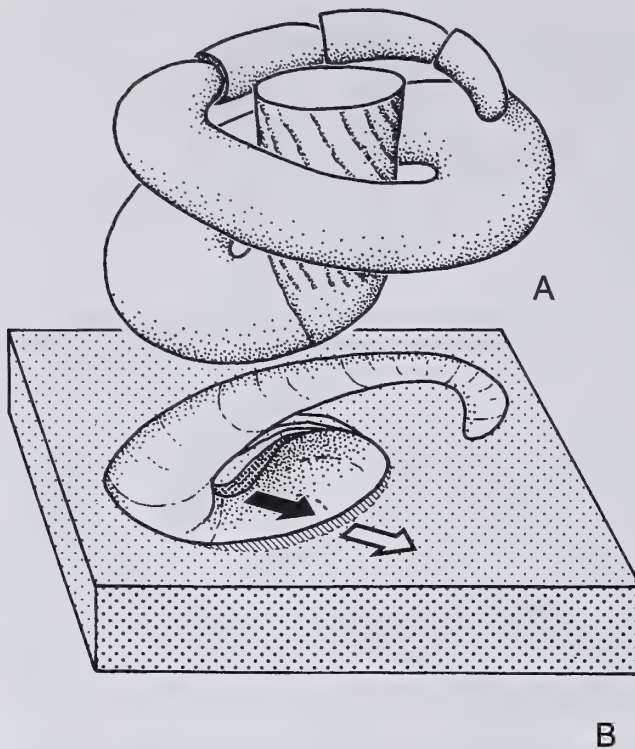
### Affinities

The anatomy of the soft parts, morphology of the operculum and general shell characteristics (above, and Figures 1, 3-5) show this species to be a member of the vermetid genus *Dendropoma* Mörch, 1861 (see also Keen, 1961). The gregarious habits and morphology of the operculum are consistent with placement in the subgenus *Novastoa* Finlay, 1927. However, as noted by Keen (1961) this subgenus may be artificial. Furthermore, *D. sp.* is conspicuously different from all other *Dendropoma* in its shell geometry, mode of growth and endolithic habit. These differences are at least as important as those on which the existing subgenera of *Dendropoma* (i.e., *Dendropoma s.s.*, *Novastoa* and *Elliptovermetus* Cossmann and Peyrot, 1922) are based. If future observations show that the shell morphology and life habits of *D. sp.* as described in this paper are a constant feature of this species, rather than an ecotypic response to a particular environment, it might be justified to erect a new subgenus to accommodate its unique character. However, a review of *Dendropoma* from the Philippines would be necessary to settle the problems connected with the specific and subgeneric placement of this genus, and such a study lies outside the scope of the present paper.

### Evolution

The evolution of the endolithic habit in *D. sp.* cannot be explained as a process characterised by a gradual increase



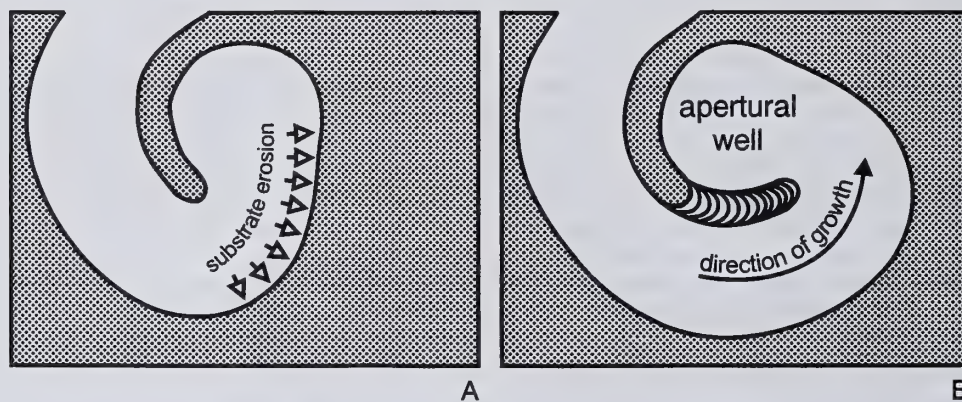


**Figure 5.** Internal mould of shell cavity (A) and cross-section through the deepest portion of the shell cavity (B), cut through a plane parallel to the surface of the substrate, in *Dendropoma* sp. In A, the early portion of the shell cavity is closed off by septa. A sculpture of coarse oblique rugae is visible on the walls of the apertural well (vertical portion of shell cavity located at the centre of the spiral). The shell aperture proper is located at the bottom of the apertural well.

in depth of the trench excavated by *Dendropoma*. This simple mechanism would produce an external roof above the whorls, which is absent in *D. sp.*

As an alternative, one could envision a growth process in which earlier portions of the shell gradually migrate deeper within the substrate during growth, by eroding substrate along one side of the shell cavity and secondarily depositing shell material on the opposite side (i.e., in a manner analogous to the sideways ontogenetic migration of the aperture). However, this process would leave telltale growth lines in the shell structure indicating earlier positions of the whorls within the substrate. This situation can be compared with the backwards and/or sideways boring process displayed by endolithic lithophagid bivalves when they move away from their original position within the substrate. This process leaves meniscus-shaped layers of calcareous material filling the vacated region of the borehole (e.g., see Savazzi, 1999b, fig. 17.2B). Such structures, instead, are absent in *D. sp.*, thus ruling out the above process and showing that the position of earlier shell portions within the substrate does not change.

A more unconventional growth mechanism (Figures 5B, 6) explains the observed features. The apertural portion of the shell, which is located at the bottom of the apertural well, grows in the manner typical of *Dendropoma*, i.e., by etching substrate along half of its circumference, and depositing shell material along the opposite half. However, in *D. sp.* the shell aperture, instead of migrating along a path parallel to the surface of the substrate, revolves around the bottom of the apertural well. As a result, the aperture rotates and progressively deepens within the substrate, leaving on the walls of the apertural well a set of spiralling, curved ridges homologous to those on the roof of semi-endolithic species (albeit arranged in a different geometric pattern because of the different trajectory of the aperture). At the same time, the rest of the shell cavity becomes coiled around the



**Figure 6.** Schematic section through the bottom portion of the shell cavity of *Dendropoma* sp. along a plane parallel to the surface of the substrate (which is located above the plane of the figure), showing the shell growth process. Substrate erosion takes place along a portion of shell cavity in proximity with the apertural well (A). The direction of growth follows a circular trajectory (arrow in B) around the apertural well, gradually moving deeper within the substrate at the same time. This process is recorded by growth lines in the shell wall that surrounds the apertural well (B). Note that, with the exception of the gradual deepening of the apertural well, neither the apertural well nor earlier coiled portions of the shell cavity change their position relative to the substrate during growth.



apertural region because it is connected to the revolving aperture by a short bent portion (Figures 5A, 6). As a result, successive whorls are located progressively deeper within the substrate, trailing behind the aperture like a spiral staircase. Instead of coiling outwards from the surface of the substrate, like regular vermetids, *D. sp.* coils into the substrate. The direction of coiling, however, remains dextral as in epifaunal vermetids. Since in all vermetids the adapical shell surface is cemented to the substrate, the different direction of translation of the whorls along the coiling axis in *D. sp.* results in an inverted direction of translation of the helicospiral. Therefore, the coiling of *D. sp.* is not sinistral as could appear from a superficial observation, but hyperstrophic dextral (see above). Early portions of the shell cavity are vacated and closed off by septa, and thus the soft parts effectively migrate deeper within the substrate, in spite of the shell being cemented to it.

This growth process achieves the combined results of deepening the apertural portion of the shell (which is the only growing shell portion, since earlier shell portions remain immobile with respect to the surrounding substrate) without moving it laterally along the surface of the substrate. In addition, it makes a fully endolithic habit possible without increasing substantially the volume of substrate that must be eroded, compared to a semi-endolithic habit. Finally, it achieves these results without requiring substantial changes in the nature of the mechanisms involved in the shell construction and growth of *Dendropoma*.

### Morphodynamics

The evolutionary process that led to this peculiar morphology and ontogeny remains to be explained. Biological morphodynamics (Seilacher, 1991) is a conceptual framework stating that the morphology and evolution of an organism can be understood as the interplay of four factors: function (i.e., all aspects of morphology with a direct adaptive significance), construction (including morphogenesis, structural materials and building principles), phylogenetic tradition (the evolutionary history, preadaptations and *Bauplan*; see below) and immediate environment (the characteristics of the environment in close proximity with the organism). The *Bauplan* is a set of constructional "building blocks" and morphologic characters that constitute the shared features of a lineage or taxonomic group (although they may not be expressed in all its members).

Morphodynamics is a recent extension of constructional morphology (*sensu* Seilacher, 1970; an alternative definition of the latter exists, but is not discussed here), which includes only the first three of the above factors. Both morphodynamics and constructional morphology were meant as practical frameworks to guide and summarise one's reasoning while carrying out an analysis of morphology, not as abstract philosophical generalisations. Therefore, the merits of these frameworks should be judged in the context of specific instances of functional analysis, like the present one.

In both conceptual frameworks, lateral migration of the shell aperture in typical *Dendropoma* is the preadaptation that allowed the evolution of the unique ontogenetic mechanism of *D. sp.* The spiral coiling of this species likewise origi-

nates from the generic gastropod *Bauplan*. While adult *Dendropoma* is facultatively not coiled, its larval shell is obligatorily coiled, just as the adult shell in noncemented ancestors of the Vermetidae was regularly coiled. Spiral shell coiling is still visible in the facultative or obligatory (albeit somewhat irregular) adult coiling of several vermetid genera (Keen, 1961; Savazzi, 1996, 1999a, and therein). Dextral shell coiling is also related to the laterally asymmetric placement of the columellar muscle in the Vermetidae (including those that are noncoiled in the adult stage). Thus, it is legitimate to state that spiral coiling is part of the vermetid *Bauplan*.

In the present case, morphodynamics may display a practical advantage over constructional morphology. The latter provides an explanation for the morphology of *D. sp.* in an adaptive context, but does not explain clearly the cause of its evolution. Morphodynamics, instead, offers a better framework for explaining both. The rock substrate inhabited by *D. sp.* is characterised by a high rate of erosion (as evidenced by grazing tracks and by the fact that early portions of the shell of this species are often eroded away; Figure 1E-F). Significantly, the only other sessile invertebrate common in the same substrate is a rock-boring foraminiferan that lives in a shallow pit (dark grey patches in Figure 1F) and continuously deepens it in order to remain protected against erosion (J. Whittaker and E. Savazzi, unpublished). It can be noticed also that the substrate is crowded (Figure 1B, E-F). These are the key environmental factors to explain the evolution of *D. sp.*

Fast erosion of the substrate encouraged a switch from a semi-endolithic to an endolithic habit, because the latter offers a better protection against erosion, and thereby an enhanced probability of survival. Most endolithic gastropods and bivalves fight erosion of the substrate by boring deeper within the substrate during growth (e.g., Savazzi, 1999a, 1999b, and references therein). This requires mainly behavioural modifications, rather than morphologic ones, since these molluscs are not cemented to the substrate, can move within their boreholes, and already bore deeper into the substrate during growth, in order to accommodate their ontogenetic increase in size. *Dendropoma*, instead, is constrained by shell cementation to the substrate in its possible evolutionary "choices".

Excavation of a deeper trench with a thicker roof (cf. Figure 2) would seem to be a straightforward route into the endolithic habit. However, this solution is not feasible because it involves a substantial increase in the volume of substrate that must be removed, and of shell material that must be secreted (i.e., the "roof" of shell material covering the trench). Alternatively, faster horizontal growth along the surface of the substrate, resulting in an increased length of the shell, would also help to fight off erosion by continually moving the organism to fresh areas of the substrate, but likewise involves an increase in the energy spent boring and secreting shell material, besides being unfeasible in crowded substrates. In *D. sp.*, a secondary return to coiling avoided these problems, and provided a working solution to seemingly contrasting necessities: cementing the organism to the substrate, allowing it to move deeper into the substrate during growth, not increasing the used surface area of sub-



strate, and not increasing the volume of removed substrate substantially, compared with a semi-endolithic habit.

The secondary return to coiling in *D. sp.* confronted this species with a "choice" between two mutually exclusive life habits: epifaunal coiling above the surface of the substrate, or endolithic coiling beneath its surface. No working intermediate choices are possible (short of abandoning coiling and reverting to an uncoiled semi-endolithic habit), because this would cause the mollusc to bore into earlier portions of its own shell, still occupied by the soft parts. Thus, the onset of coiling and of fully endolithic habits must have been a sudden evolutionary event, made possible by the facts that coiling was already available in the vermetid Bauplan, and that the accompanying coadaptations did not require the evolution of substantially new morphological or behavioural traits.

Alternatively, an intermediate paedomorphic stage, adaptive in lessening the negative effects of erosion by reducing the life span, may have been involved. Such a stage likely had a life habit comparable to that of juvenile vermetids, and therefore displayed no substantial morphologic innovation. The subsequent return to a larger size forced a switch from epifaunal to endolithic habits and hyperstrophic coiling. Thus, also this alternative process involves a sudden evolutionary change.

The facts that several species of *Dendropoma* display facultative or obligatory epifaunal coiling (see above), while all *Dendropoma* are capable of semi-endolithic boring, suggest an evolutionary scenario in which epifaunal coiling was initially lost in *Dendropoma*, and subsequently reappeared secondarily multiple times during the evolution of this genus, rather than representing the uninterrupted maintenance of this character from epifaunal ancestors. The factor that "tipped the scales" in favour of endolithic boring in *D. sp.*, instead of resulting in yet another instance of parallel evolution of epifaunal coiling, is likely the substrate being subjected to a high rate of wave erosion and/or bioerosion, which makes epifaunally coiled individuals excessively vulnerable. Thus, the immediate environment appears to be the trigger of the evolutionary processes that led to the unique shell morphology and growth mechanism in *D. sp.* In turn, the presence of a solid substrate surrounding the organism, which characterises the endolithic environment, allowed the evolution of a growth mechanism that would be impossible in an epifaunal organism.

To the knowledge of the writer, the clavagellid bivalve *Bryopa* is the only other boring mollusc that permanently cements the shell (in particular, the left valve) to the substrate without losing the capability of migrating deeper within the substrate during growth (Savazzi, 2000). *Bryopa* does so by continuously elongating the shell and shifting the position of the soft parts within the left valve, abandoning its early portions. Thus, its adaptations are partly convergent with those of *D. sp.*

### Conclusions

*Dendropoma sp.* is unique among vermetids in being fully endolithic in the adult stage. During the juvenile, semi-endolithic stage, it builds a broadly umbilicated whorl partly

embedded in the substrate. Subsequently, instead of building successive whorls upward and elevating its shell above the substrate, as in several epifaunal vermetids, it places new whorls deeper within the substrate and underneath earlier ones, like a descending spiral staircase. The aperture moves into the shell umbilicus and does not migrate further along the surface of the substrate during growth. Instead, it gradually deepens within an umbilical apertural well. This process results in the formation of a characteristic spiralling pattern of ridges on the walls of the well.

While the shell morphology of *D. sp.*, at first sight, appears to violate the fundamental laws of gastropod shell geometry, the adaptiveness and evolution of this morphology can be successfully explained within the framework of biological morphodynamics. The demands posed by a substrate subjected to rapid erosion appear to be the factor that triggered the evolution of this form. Its growth mechanism and most of its unique adaptations are related to the sudden change in immediate environment caused by an evolutionary switch from a semi-endolithic to a fully endolithic life habit. This switch was a sudden event, because the preadaptations of *Dendropoma* allow no feasible intermediate stage between a semi-endolithic and a fully endolithic life habit.

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## External features of embryonic and early postembryonic shells of a Carboniferous goniatite *Vidrioceras* from Kansas

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**Abstract.** The ornamentation and dorsal wall structure of *Vidrioceras* (Cycloloboidea, Goniatitina) in the early ontogenetic stage are described on the basis of specimens from the Upper Pennsylvanian in Kansas, USA. The exposed surface of the embryonic shell is smooth, without any trace of ornamentation or growth lines. Regularly spaced lirae abruptly appear on the early postembryonic shell just adoral of the primary constriction. The inner surface of the dorsal wall in the embryonic and early postembryonic stages exhibits a distinct ornament consisting of evenly spaced, longitudinal ridges, which are replaced adorally by the typical wrinkled ornament in the subsequent stage. Our observations are in accord with those of goniatites from the Upper Carboniferous Buckhorn Asphalt of Oklahoma, suggesting that in the Goniatitina, the outer surface of the embryonic shell is smooth. Comparison with the embryonic shell formation of extant *Nautilus* suggests that in the Goniatitina, the embryonic shell was uniformly secreted by the shell gland on the posterior side of the embryo.

**Key words:** Ammonoidea, Carboniferous, development, embryonic shell, Goniatitina, Kansas, *Vidrioceras*

### Introduction

The embryonic shell of ammonoids (termed the ammonitella by Druschits and Khiami, 1970) consists of a spherical initial chamber and approximately one subsequent whorl with a thick nacreous swelling (primary varix) at the aperture (for references see Landman *et al.*, 1996). The boundary between embryonic and postembryonic stages is marked by the primary constriction. Most previous studies on the external morphology and microstructure of embryonic shells of the Ammonoidea have been based on Mesozoic material with aragonitic preservation (Druschits and Doguzhaeva, 1981; Bandel, 1982, 1986; Bandel *et al.*, 1982; Landman, 1982, 1985, 1987; Landman and Bandel, 1985; Tanabe, 1989; Kulicki and Doguzhaeva, 1994; Landman *et al.*, in press, among others). In Paleozoic ammonoids, the microstructure of the embryonic shell is rarely preserved in most fossils due to diagenesis, except for aragonitic

goniatites studied by Kulicki *et al.* (in press) from the Carboniferous Buckhorn Asphalt in Oklahoma, USA. Previous authors have indicated that the embryonic shells of Paleozoic ammonoids display ornamentation and features of several internal shell characters different from those of Mesozoic ammonoids (Beecher, 1890; Miller, 1938; House, 1965; Mapes, 1979; Tanabe *et al.*, 1993, 1994; Doguzhaeva, 1996; Landman *et al.*, 1996; Landman *et al.*, 1999; Klofak *et al.*, 1999; Kulicki *et al.*, in press). These studies have revealed a variety in the embryonic shell features in the Ammonoidea that can be used for higher-level phylogenetic analysis.

In this paper, we describe the ornamentation and the dorsal wall structure of goniatites at the embryonic and early postembryonic stages based on specimens from the Upper Pennsylvanian of Kansas, USA. Furthermore, the result of our observations is compared with data on other ammonoids and extant *Nautilus* and discussed for its implications for



systematics and embryonic shell formation. Some of the specimens utilized have been studied by Tanabe *et al.* (1993), but those observations are partly reevaluated in this paper.

### Material and methods

Tanabe *et al.* (1993) discovered an embryonic ammonoid assemblage in a carbonate concretion recovered from the Virgilian (Upper Pennsylvanian) offshore shale in Pomona, Kansas, USA. These authors classified the embryonic ammonoids into two morphotypes by the difference in the size and shape of their initial chambers, namely into a large and globular and a small and ellipsoidal one. They further assigned these large and small morphotypes to *Vidrioceras* (Vidrioceratidae, Cycloloboidea) and *Aristoceras* (Thalassoceratidae, Thalassoceratoidea) respectively, on the basis of comparison with their initial chambers with those of larger specimens of these two genera from the same concretion.

About one hundred well preserved specimens of the two genera at embryonic and early postembryonic stages were removed without etching from the weathered portion of the concretion by the wet-sieving method. They were coated with platinum and observed by scanning electron microscopy. Although the embryonic shells of *Aristoceras* occur more abundantly than those of *Vidrioceras*, we did not observe early shell features of the former genus because of poor preservation of the dorsal wall sculpture in the available specimens. As already pointed out by Tanabe *et al.* (1993), the goniatite specimens from Pomona preserve calcified shell material, and the recrystallized condition of their shell wall prevents study of the shell ultrastructure. Our observations are, therefore, mainly restricted to the external features of these specimens. All of the specimens utilized are housed in the University Museum, the University of Tokyo (UMUT).

### Observations

#### Embryonic shells

*General morphology and ornamentation.*— The embryonic shells of *Vidrioceras* examined are all globular in overall shape and consist of a spindle-shaped initial chamber and approximately one subsequent planispiral whorl (Figure 1). In median section, a thick nacreous swelling (primary varix) appears on the inner side of the prismatic layer in the apertural region (see Tanabe *et al.*, 1995, figure 2A). The first whorl is much broader than high, covering the greater portion of the initial chamber (Figures 1, 2). The spiral length of the embryonic shell (=ammonitella angle of Landman *et al.*, 1996) is relatively long, measuring about 360° in median section. The embryonic shell diameter in the specimens examined ranges from approximately 720  $\mu\text{m}$  (UMUT PM19872-1; Figure 1.1) to 780  $\mu\text{m}$  (UMUT PM19872-3; Figure 1.3a). The exposed surface of the shell at the embryonic stage is smooth without any trace of ornamentation or growth lines (Figure 1).

*Dorsal wall of the first whorl.*— In several embryonic and early postembryonic specimens, part of the first whorl has

been lost due to mechanical destruction during the taphonomic process or due to the wet-sieving procedure. In those specimens, evenly spaced longitudinal ridges are visible on the dorsal side of the missing whorl portion (Figures 2.1–2.3, 3.1, 3.2). They never occur on the lateral flanks of the initial chamber that are free from the first whorl. This fact indicates that the longitudinal ridges represent the sculpture on the inside surface of the dorsal wall of the first whorl. A weaker ridge is occasionally intercalated between the longitudinal ridges (Figure 2.3b).

*Remarks.*— Tanabe *et al.* (1993, fig. 3A) described evenly spaced longitudinal ridges on the ventrolateral side of several embryonic shells of *Vidrioceras* from the same locality and interpreted them as the surface ornamentation. However, our reexamination of these and additional specimens reveals that the longitudinal ridges are not the surface ornamentation but the microornamentation on the inner side of the dorsal wall, and that the exposed surface of the embryonic shell of *Vidrioceras* is in fact smooth.

#### Early postembryonic shells

The embryonic shell margin is easily visible from outside by the presence of the slightly depressed primary constriction followed by the sharp apertural edge (see arrows, Figure 1.1, 1.3a). Fine transverse lirae abruptly appear on the adoral side of the primary constriction. They are initially rectiradial in the early postembryonic stage (Figure 1.1, 1.3a, b), but become prorsiradial and gently convex at the venter in a later stage. Each lira is asymmetric in cross section with a steep edge on the adoral side and is gently inclined adapically (Figure 1.3b).

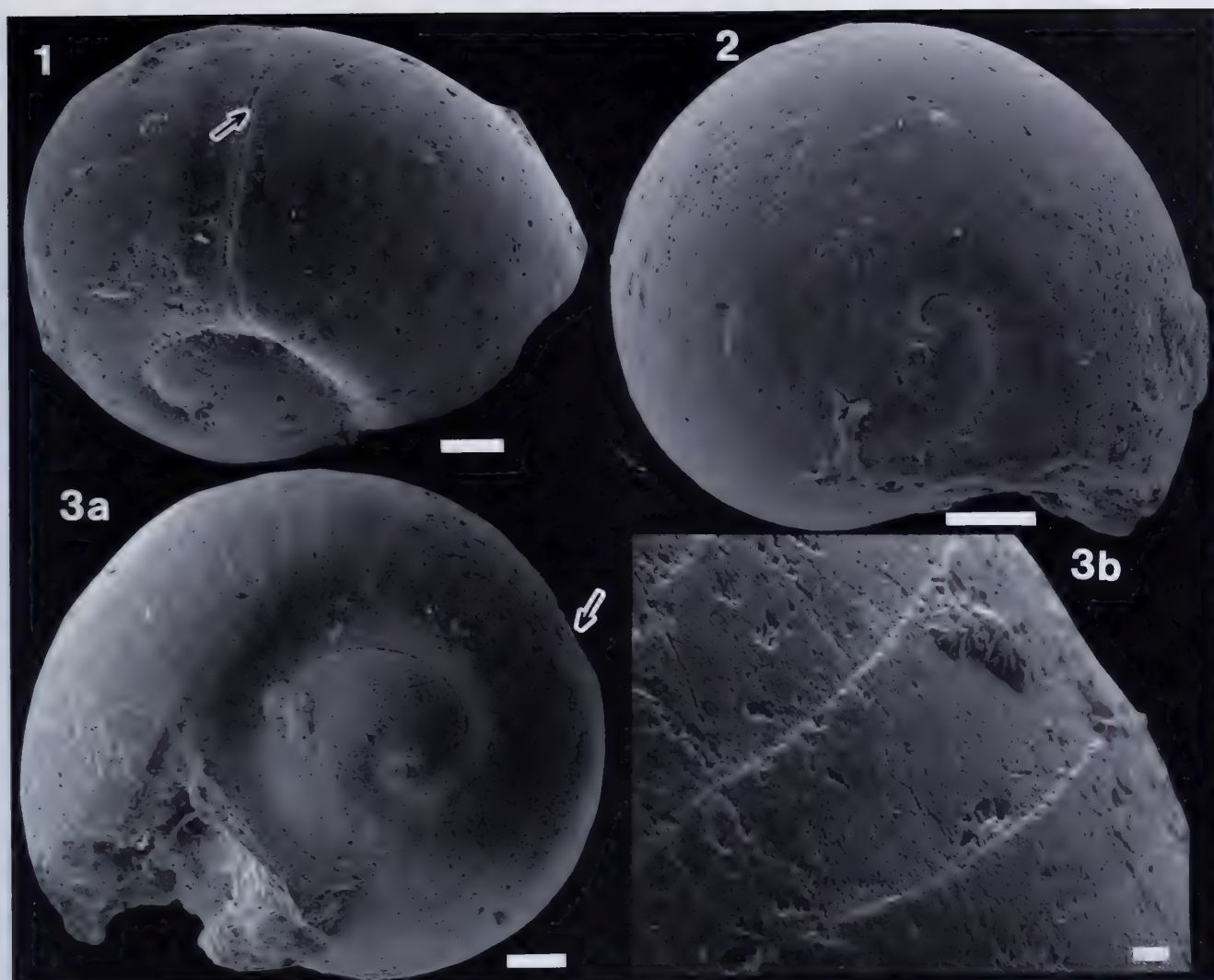
The change of the inner surface sculpture of the dorsal wall is visible in several early postembryonic shells whose body whorl is partly lost secondarily (Figure 2.1–2.3). In one of these specimens, shown in Figure 2.2, the longitudinally ridged ornament disappears on the dorsal side of the embryonic shell aperture and a wrinkled ornament similar to a human fingerprint pattern begins to appear on the adoral side of the primary constriction. In the embryonic or early embryonic specimen shown in Figure 2.4, the wrinkled ornament already exists on the dorsal side near the shell margin. In another two specimens, shown in Figure 2.1 and 2.3, the longitudinally ridged ornament extends for a half whorl beyond the primary constriction. These observations clearly indicate that *Vidrioceras* exhibits some variation in the ontogenetic change of the dorsal wall ornament.

#### Comparison with other ammonoids

On the basis of observations on excellently preserved material from the Pennsylvanian (Desmoinesian) Buckhorn Asphalt in Oklahoma, Kulicki *et al.* (in press) reported that the outer surface of the embryonic shells of goniatites is smooth without any trace of ornamentation or growth lines, as is the case of *Vidrioceras* described herein. These observations strongly suggest that in the Goniatitina the embryonic shell is smooth.

Ornamentation on embryonic shells of the Goniatitina differs from those of other ammonoid suborders. In the Devonian Agoniatitina, Anarcestina and Tornoceratina, the



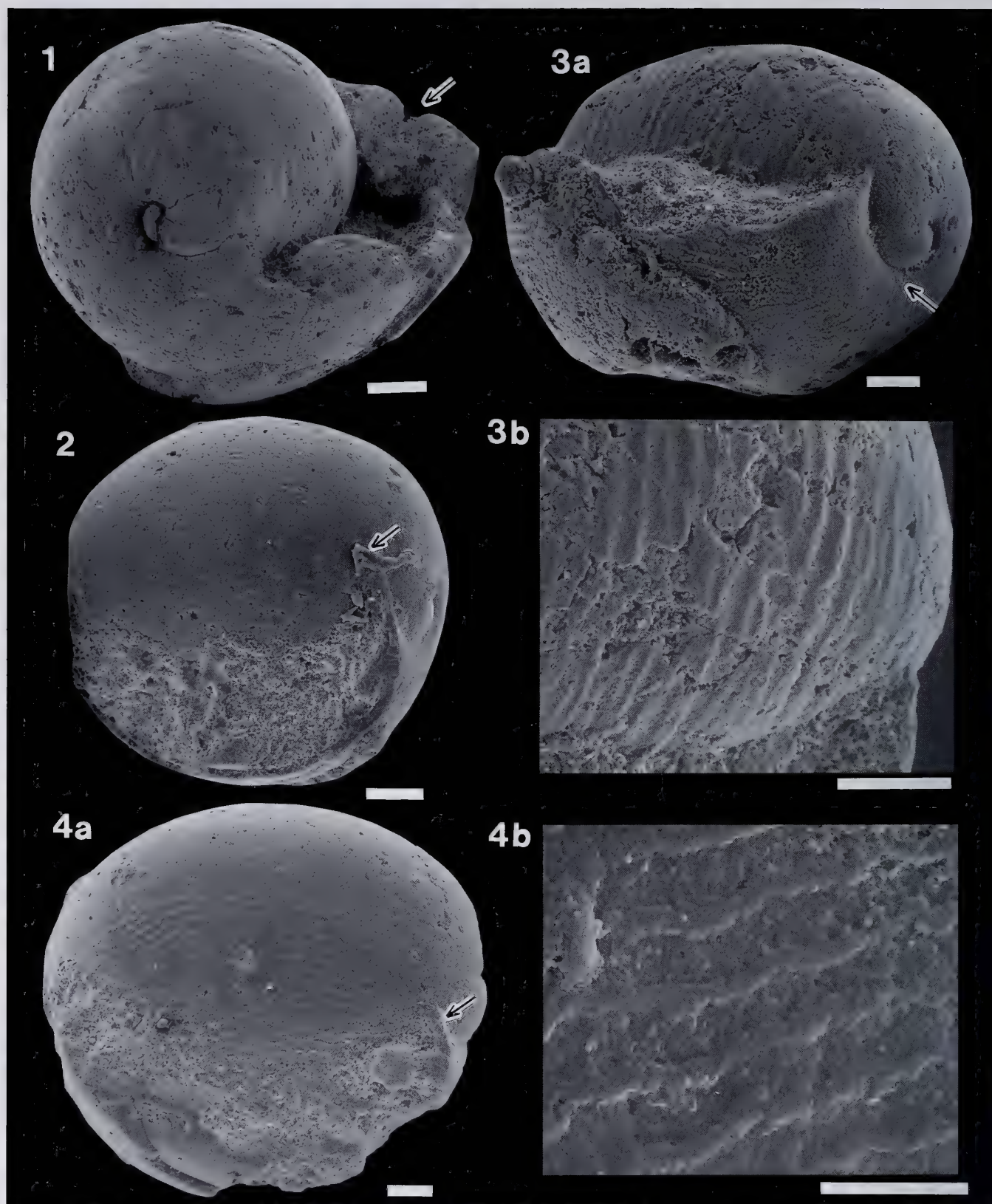


**Figure 1.** *Vidrioceras* sp. 1. Oblique view of early postembryonic specimen showing slightly depressed primary constriction and adjacent embryonic shell edge (pointed to by an arrow). The embryonic shell is smooth, while the postembryonic shell is sculptured by fine transverse lirae. UMUT PM19872-1. 2. Lateral view of embryonic shell with smooth surface. UMUT PM19872-2. 3a, b. UMUT PM19872-3. Lateral view of early postembryonic shell showing abrupt appearance of fine transverse lirae after primary constriction (pointed out by an arrow) (3a) and close-up of lirae (3b). Scale bars: 100 µm (1, 2, 3a) and 10 µm (3b)

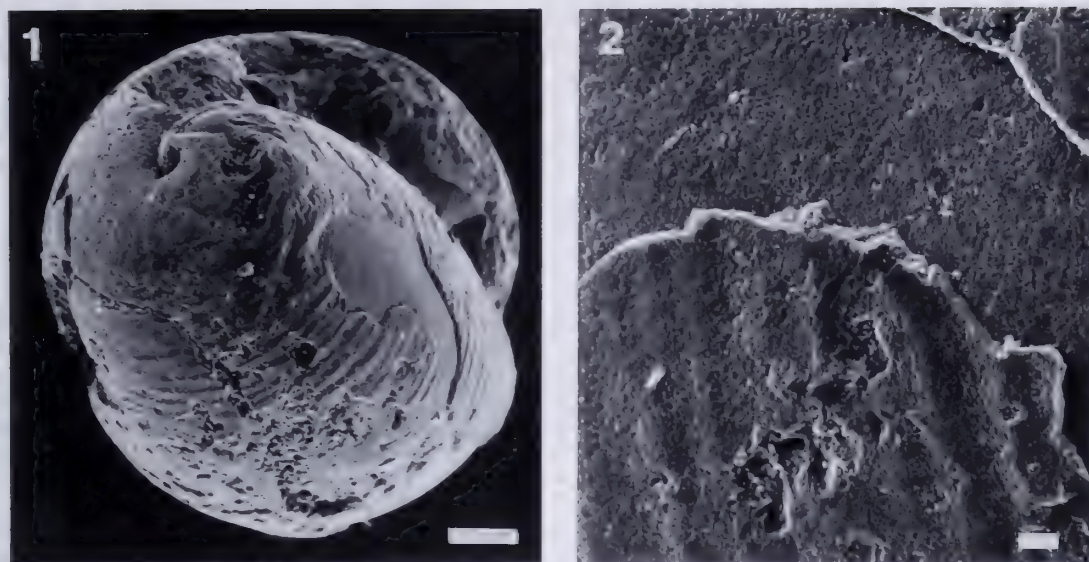
embryonic shells are characterized by fine transverse lirae parallel to the aperture (Beecher, 1890; Miller, 1938; House, 1965; Landman *et al.*, 1996; Klofak *et al.*, 1999). In the uncoiled Late Silurian and Devonian Bactritina and partly coiled Devonian ammonoids, the straight whorl after the initial chamber is also covered with transverse lirae (Erben, 1964). Mapes (1979) reported both smooth and longitudinal ornament on the initial subspherical chamber and early shaft of "bactritids" from the Carboniferous, and Mapes (1979) and Doguzhaeva (1996) reported a reticulate ornamentation on the earlier embryonic shaft portion of "bactritids" from the Carboniferous and Permian, respectively. However, Doguzhaeva *et al.* (1999) suggested that some of these specimens may eventually be reassigned to

the Coleoidea. In the Ceratitina, Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina, the embryonic shell lacks lirae and instead is covered with minute tubercles (Kulicki, 1974, 1979; Bandel, 1982, 1986; Bandel *et al.*, 1982; Landman and Waage, 1982; Landman, 1985, 1987; Tanabe, 1989; Kulicki and Doguzhaeva, 1994; Landman *et al.*, in press). To sum up these previous descriptions, at least three kinds of embryonic shell ornamentation have been recognized in the Ammonoidea excluding Upper Paleozoic "bactritids". Each ammonoid suborder, excluding the doubtful taxon Bactritina, appears to have its own characteristic pattern of ornamentation.









**Figure 3.** *Vidrioceras* sp. **3a.** Oblique view of embryonic shell with preserving interior dorsal wall sculpture of the first whorl with longitudinal ridges. **3b.** Close-up of longitudinal ridges on interior side of dorsal wall. Note that the boundary between ventral and dorsal shell walls is discernible in this specimen. UMUT MM19872-8.

### Discussion

Observations of the early embryonic shells of extant *Nautilus* provide a reference point for discussions about the embryonic development of ammonoids. According to Arnold and Landman (1993) and Tanabe and Uchiyama (1997), the early embryonic shell development of *Nautilus* can be divided into two stages with different shell microstructure and ornamentation. In the first stage (=early organogenetic stage), a low cap-shaped shell with a distinct median depression (called cicatrix) is secreted in the sequence of outer conchiolin and inner prismatic layers. The cicatrix lacks growth lines, indicating uniform shell secretion by the mantle primordium (shell gland) on the posterior side of the embryonic body (see Tanabe and Uchiyama, 1997, fig. 1A). In the second stage (=middle organogenetic stage), a new shell consisting of outermost conchiolin, outer prismatic, middle nacreous, and inner prismatic layers appears at the outer margin of the cicatrix, leaving a discontinuity in the shell structure at the boundary. It is sculptured by transverse growth lines and radial undulations. At this stage of development, the anterior mantle margin is well differentiated and possesses three folds, where shell secretion

occurs (Tanabe *et al.*, 1991).

The absence of transverse lirae on the embryonic shells of the Goniatitina strongly suggests that the walls of the initial chamber and the first whorl were secreted synchronously by the undifferentiated shell gland. Bandel (1982) and Kulicki and Doguzhaeva (1994) hypothesized this kind of embryonic shell development in Mesozoic ammonoids, relying upon observations about the biomineralization of embryonic shells of modern "archaeogastropods". The longitudinal dorsal layer was probably secreted at a late stage of embryogenesis and occasionally at an early postembryonic stage. The appearance of transverse lirae on the postembryonic shell indicates an accretionary mode of growth. This event does not occur synchronously with the development of the dorsal wall with wrinkled ornamentation (Figure 2.1–2.4; Kulicki *et al.*, in press, pl. 2, fig. 3). Such a wrinkled dorsal wall has been extensively recognized in Paleozoic ammonoids in the postembryonic stage (House, 1971; Walliser, 1970). Kulicki (1979, 1996) and Kulicki *et al.* (2001) have pointed out that the dorsal wall of ammonoids consists of two components, namely, the outer component consisting of organo-prismatic material, sometimes with a wrinkled texture on the outside, and the inner prismatic component that covers the outer

← **Figure 2.** *Vidrioceras* sp. **1.** Lateral view of incomplete postembryonic shell, part of whose body whorl is lost. Dorsal wall of the first-second whorls exhibits longitudinally ridged ornament on the inner side. UMUT MM19872-4. **2.** Ventral view of early postembryonic shell showing change of interior dorsal wall sculpture from longitudinally ridged pattern to wrinkled pattern at embryonic shell/postembryonic shell boundary. UMUT MM19872-5. **3a, b.** UMUT MM19872-6. **3a.** Oblique view of incomplete postembryonic shell, showing change of interior dorsal wall sculpture from longitudinally ridged pattern in embryonic stage to wrinkled pattern in postembryonic stage. **3b.** Close-up of longitudinally ridged dorsal wall structure in early postembryonic stage of same specimen. **4a, b.** UMUT MM19872-7. **4a.** Ventral view of embryonic (or early postembryonic) shell showing interior feature of dorsal wall with wrinkled ornamentation. **4b.** Close-up of wrinkled ornamentation in same specimen. Scale bars: 100  $\mu$ m (1–4a) and 40  $\mu$ m (4b). Arrows in 1, 2, 3a, and 4a point to the approximate position of primary constriction.



component on the adapical side of the body chamber. Our observations indicate that the inner dorsal wall component is absent in the embryonic shells of *Vidrioceras*. It presumably begins to appear in the postembryonic stage.

In view of the absence of transverse lirae, the mode of embryonic shell formation in the Ceratitina, Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina may also be explained by the "archaeogastropod model" of Bandel (1982) and Kulicki and Doguzhaeva (1994). The presence of fine transverse lirae on the relatively large embryonic shells of the Devonian suborders Agoniatitina, Anarcestina and Tornoceratina and on their postembryonic shells (see Landman *et al.*, 1996, appendix I) is, however, problematic. One possibility is that in the embryonic stage the mantle already was differentiated in the embryonic stage to secrete a shell with growth lines at its anterior margin. This type of embryonic shell development would be described as accretionary growth. A second possibility is that the embryonic shell was rapidly mineralised and an accretionary mode of growth characterized only the postembryonic shell (Klofak *et al.*, 1999). Future research utilizing well preserved material will resolve this problem.

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# Macro- and microstructure of shell and operculum in two Recent gastropod species, *Nerita (Theliostyla) albicilla* and *Cinnalepeta pulchella* (Neritopsina: Neritoidea)

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**Abstract.** The shell and opercular structures of *Nerita (Theliostyla) albicilla* and *Cinnalepeta pulchella* were described and compared with those of other extant members of Neritopsina. The shell of *N. (T.) albicilla* is composed of four layers: the outermost prismatic layer, followed by the simple crossed-lamellar layer, the myostracum, and the inner complex crossed-lamellar layers. The operculum consists of three prismatic layers deposited on both sides of an organic layer. *C. pulchella* also has a four-layered shell, but lacks an operculum. The outer layer is a homologous structure. The shells of Recent neritopsine families can be categorized into a four-layered group (Neritiliidae, Neritidae, and Phenacolepadidae) and a three-layered group (other families). In contrast, opercular structure is markedly variable in the Neritopsina, and little correlation can be established in the light of phylogenetic evolution or adaptation.

**Key words:** Neritidae, Neritopsina, operculum, Phenacolepadidae, shell structure

## Introduction

Neritopsina is a phylogenetically distinct gastropod clade which originated in the Ordovician (Bandel and Frýda, 1999). The Recent members share characteristic apomorphies of odontophoral cartilages and muscles, anterior digestive tract, reproductive organs, and nervous system (Haszprunar, 1988; Ponder and Lindberg, 1997; Sasaki, 1998) and exhibit successful adaptive radiation in a wide range of habitats in deep-sea hydrothermal vent or hydrocarbon seep, submarine cave, intertidal rocky shore, and nonmarine aquatic and terrestrial environments (Ponder, 1998; Sasaki, 1988). It is also particularly interesting that neritopsines have rich fossil records since the early Paleozoic (Bandel, 1992; Bandel and Frýda, 1999), and that ancient taxa like *Neritopsis* have survived as relics in cryptic habitats (Kase and Hayami, 1992).

Among hard-part characters, shell structure, along with larval shell morphology, is of primarily taxonomic importance for studies uniting fossil and Recent taxa of Gastropoda (Bandel, 1982; 1988; 1991; Bandel and Geldmacher, 1996). In Gastropoda, Patellogastropoda are known to exhibit remarkable diversification of the shell microstructure (MacClintock, 1967; Lindberg, 1988, 1998). Grouping by

shell structure corresponds well to the anatomical division of supraspecific taxa, and therefore enables paleontologists to allocate fossilized taxa within an anatomy-based systematic scheme (Kase, 1994; Kase and Shigeta, 1996; Lindberg and Hedegaard, 1996; Hedegaard *et al.*, 1997). As for other gastropod higher taxa, Vetigastropoda are typically characterized by the apomorphic occurrence of columnar nacreous structure, although some taxa have supposedly lost it secondarily (Hedegaard, 1997). In the Apogastropoda, which is a huge clade including Caenogastropoda and Heterobranchia, the shells are composed primarily of several layers of crossed-lamellar structure and differences between distantly related subclades within it are in general minor (Bøggild, 1930; Bandel, 1979; Togo and Suzuki, 1988). At relatively lower rank, however, some striking differences can be revealed by detailed comparison, as was shown in littorinid genera by Taylor and Reid (1990).

Despite its unique phylogenetic status among gastropods, little discussion has been devoted to exoskeletal evolution of Neritopsina as compared to other major taxa of molluscs. The current knowledge of neritopsine hard-part structures is derived from only a limited amount of literature, and in addition, most data have been documented in simple format with a few or no illustrations. To increase data quality and

quantity on neritopsine hard parts, this study aims to describe the shell and opercular structures of two Recent species in detail from the macro- to microscopic level. The results of the observations were compared with the published data of other neritopsines in the literature, and their similarities and dissimilarities were discussed from phylogenetic and adaptational viewpoints.

### Material and methods

The shells of *Nerita (Theliostyla) albicilla* were collected alive from an intertidal zone at Banda, Tateyama, Chiba Prefecture, central Japan, and living specimens of *Cinnalepeta pulchella* from Tosashimizu, Kochi Prefecture, southwest Japan were provided by Dr. Shigeo Hori. In the laboratory, the macroscopic morphology and the distribution of shell layers based on texture were first observed under a binocular microscope. Then, the shell was crushed with a hammer, and the original position of fragments was labeled before cleansing in bleach for 12 hours and later in running water for 30 minutes. The fresh fracture of shell fragments was observed with a scanning electron microscope (SEM).

The description of microstructure was made on layer distribution, boundary between layers, form of crystal aggregation, and orientation and morphology of first- to third-order units (major to minor structural arrangement). The descriptive terminology of microstructure follows Carter and Clark (1985) and Kano and Kase (2000b). The two terms, "crossed lamellar" and "complex crossed lamellar," are abbreviated as "CL" and "CCL."

Terms for orientation were based on the following criteria: (1) "anterior-posterior" direction was determined by body axis of the animal, and (2) "adaxial-abaxial" distinction relative to coiling axis of whorls was used to indicate relative position along inner-outer lips of the aperture.

The samples used in this study are preserved in the University Museum, the University of Tokyo (UMUT).

### Description

Order Neritopsina Cox and Knight, 1960

Superfamily Neritoidea Rafinesque, 1815

Family Neritidae Rafinesque, 1815

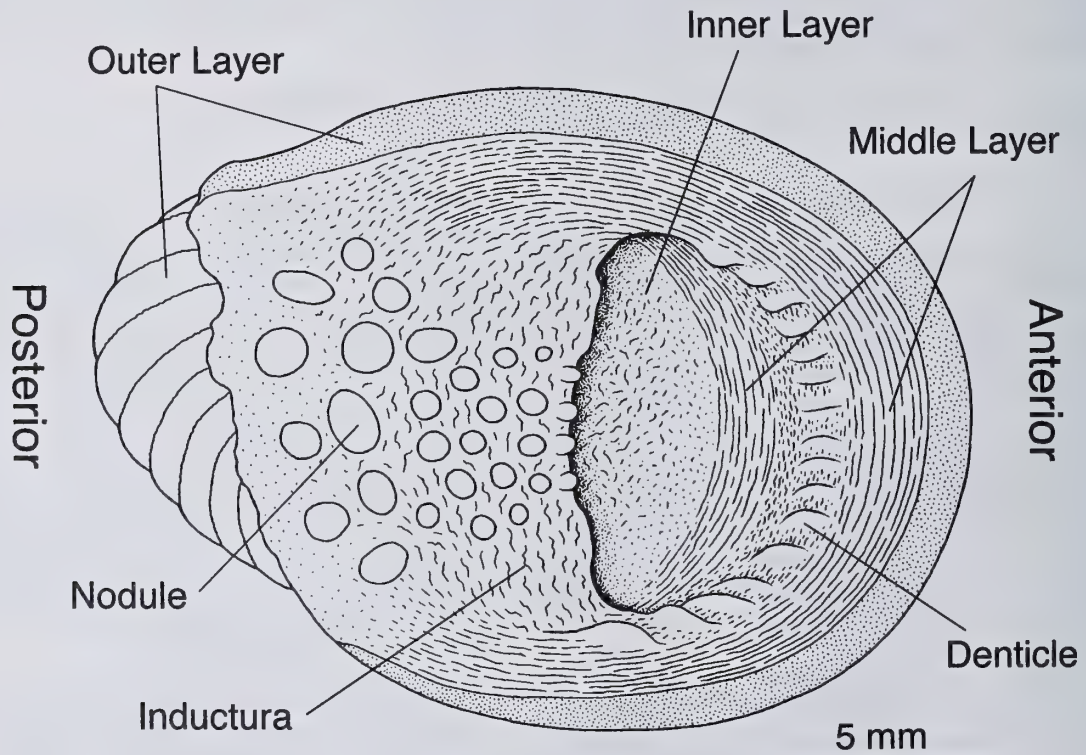
*Nerita (Theliostyla) albicilla* Linnaeus, 1758

Figures 1–5

**Shell.**—The shell is elongate along the anterior-posterior axis of the animal. The spire is completely depressed as a part of rounded whorls, and the external part of the shell is mostly occupied by a large body whorl and an extended aperture.

The outer lip of the aperture is thickened and indented with elongate denticles, being arranged parallel to the apertural margin. The inner lip spreads widely over the body whorl to form a robust inductura.

The shell wall near the outer lip consists of three layers;



**Figure 1.** Apertural view of the shell of *Nerita (Theliostyla) albicilla*. The sculpture and texture of the surface are depicted slightly schematically. The dark outer layer is distinguished by fine-grained smooth surface, the middle layer exhibits dense linear pattern of CL structure, and most of the inner layer is visible as irregularly oriented lines.



i.e. outer and middle layers and a distinct denticular zone (Figure 1). The outer layer contains black pigments, encircles the apertural margin, and makes a clear contrast with the pale inner layer. Microstructurally this layer is formed of a thick aggregate of short prisms (Figure 3A), which can be identified as blocky prismatic structure. The prisms attain less than 4  $\mu\text{m}$  in length and 1  $\mu\text{m}$  in width. The middle layer is composed of comarginal simple CL structure (Figure 3B–E). The linear lines of the first-order units are clearly visible on the inside of the aperture even at low magnification (Figures 1, 2). The denticular zone is built up of a thin layer of irregularly crossed fine crystals (CCL structure). The denticles do not continue spirally toward the inside of the aperture but remain in the identical position due to resorption.

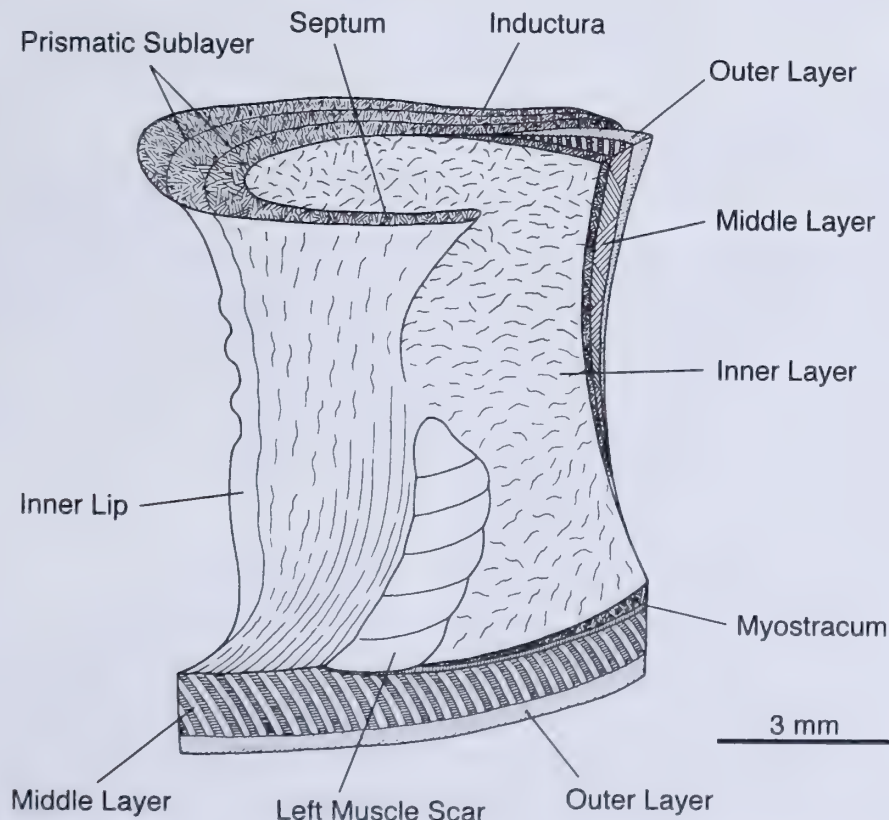
The inner lip margin is shallowly curved with two to four small nodules (Figure 1). The surface of the inductura is roughened with nodules of various size, and their number and distribution are considerably variable intraspecifically. The inductura, especially near the inner lip, shows an irregular texture reflecting the first-order arrangement (Figure 1). There is no sharp boundary between the CL structure of the middle layer and the CCL structure of the inductura. The linear patterns of the middle layer gradually merge into the irregular patterns of the inductura (Figure 1).

Shell muscle scars are separated into a disjunct pair corresponding to right and left shell muscles (see Sasaki, 1998:

fig. 73a). The left scar is located on the basal side near the inner lip (Figure 2), while the right one lies on the opposite, apical side. The scars are deeply impressed on the interior shell surface and reflect the form of muscles which are divided into bundles (Figure 2). The myostracum from the left scar is formed as a vertical stack of irregular prisms (Figure 3F), and its thickness exceeds 80  $\mu\text{m}$  in an adult shell. The myostracum from the right scar is immediately resorbed and not traceable in most sections.

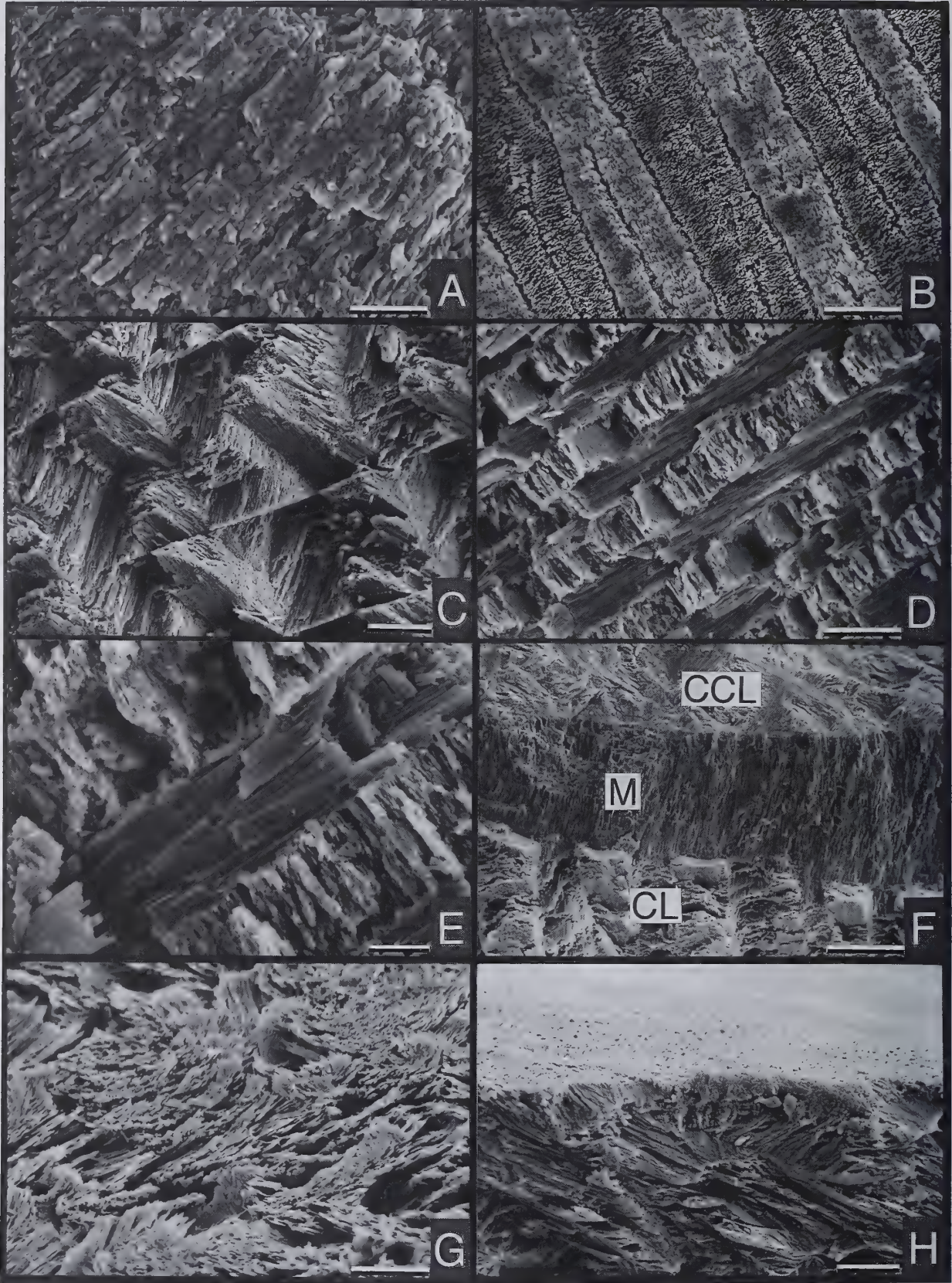
The inside of the visceral part of the shell is extensively resorbed and reorganized as a hollow space without a true columella. A platy septum connecting the inner lip and apical wall of the shell is secreted and inserted into the narrow space between head-foot and uncoiled visceral mass of the animal (Figure 2; see also Sasaki, 1998: fig. 73a). The septum, inner lip, inductura, and the interior of whorls are all constructed as a continuity of the inner layer (Figure 2). The layer has CCL structure: lathy third-order units are set radially to form fan-shaped second-order units, which in turn are vertically stacked to form wedgelike first-order units which are irregularly oriented and interdigitate with one another (Figure 3G, H). The structure appears as spinous crossing prisms at the initial stage of formation near its growth front. Several very thin prismatic sublayers are inserted in a thick CCL layer of the inductura (Figure 2).

**Operculum.**—The operculum is heavily calcified with a distinct apophysis (Figure 4A, B). The exterior surface is

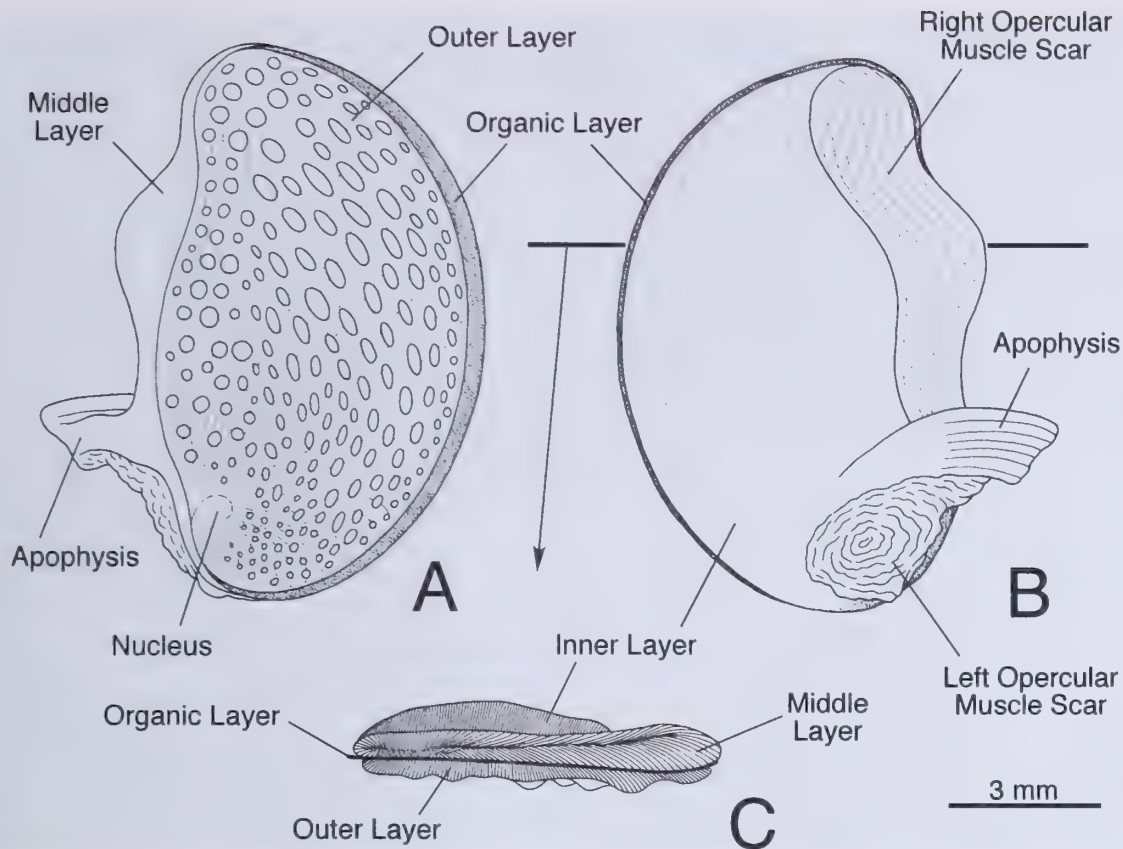


**Figure 2.** Schematic representation of inner part of whorls of *Nerita* (*Theliostyla*) *albicilla*, seen from the outer lip of the aperture. Shell layers on cut planes are illustrated based on the results of observations with SEM.









**Figure 4.** Operculum of *Nerita* (*Theliostyla*) *albicilla*. **A.** Exterior view. **B.** Interior view. **C.** Vertical section showing the growth direction of prisms in three calcified layers. Cut position is shown in Figure B with solid lines.

covered with small nodules which tend to be arranged spirally (Figure 4A). The nucleus lies on the adaxial basal side at the origin of the spiral growth line.

The calcified part of the operculum can be divided into three layers (Figure 4C). The outer and inner layers are both composed of slightly inclined, nearly vertically ordered prisms (Figure 5B, D). In the middle layer, prismatic crystals are arranged in a spherulitic form (Figure 5C). A very thin organic layer, the homologue of the noncalcified operculum of other gastropods, is mostly concealed between the outer and middle layers and appears only along the abaxial margin (Figure 4A, B).

The adaxial side of the operculum is partially embedded in the pedal musculature of the animal and marks clear depressions of muscle scars (Figure 4B). The left scar is small and very irregular with nearly concentric lines (Figure 5A). The right scar is elongated along the abaxial margin and smoothened.

Family Phenacolepadidae Rafinesque, 1815  
*Cinnalepeta pulchella* (Lischke, 1871)

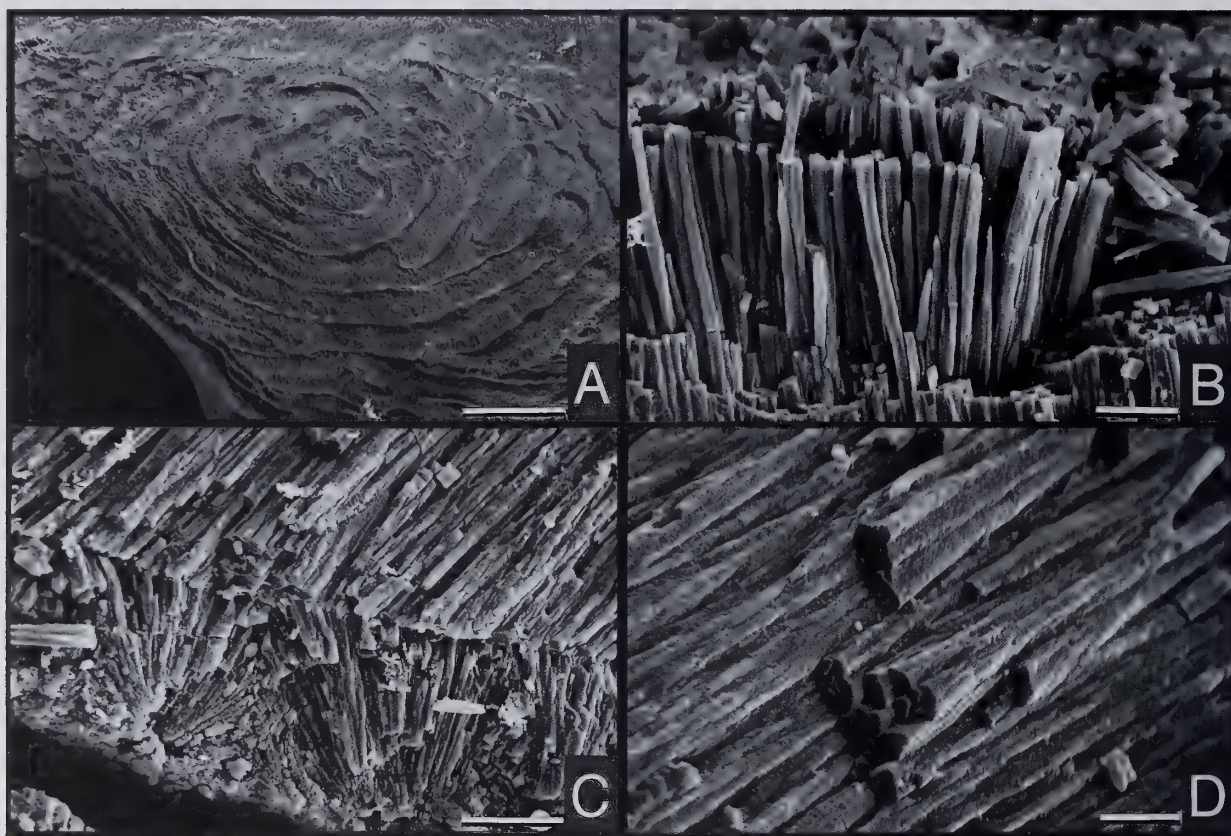
Figures 6, 7

**Shell.**—The shell is completely limpet-shaped and elongated along the anterior-posterior axis (Figure 6). The apex is situated at the posterior end of the shell. The larval shell in the original position of the apex is involved between whorls and inner lip during growth and no longer visible in a fully matured adult shell. The inside of the apex is slightly remoulded by resorption, but a septumlike structure is not constructed in this species.

The shell consists of four layers, including the myostracum. The outer layer is composed of fine homogeneous crystals (homogeneous structure) (Figure 7A, B). The middle layer is of commarginal simple CL structure. It is somewhat transparent, and clearly demarcated from the

◀ **Figure 3.** SEM micrographs of shell microstructure of *Nerita* (*Theliostyla*) *albicilla* (UMUT RM27950). **A.** Blocky prismatic structure of outer layer. Scale = 5  $\mu$ m. **B.** Outcrop pattern of simple CL structure near outer lip of aperture. Scale = 20  $\mu$ m. **C.** Oblique view of the fracture of simple CL structure in the middle layer. Scale = 20  $\mu$ m. **D.** Horizontal view of the fracture of the same layer. Scale = 20  $\mu$ m. **E.** Enlarged view of the same layer, showing the arrangement of the third-order units of CL structure. Scale = 5  $\mu$ m. **F.** Vertical fracture of the myostracum inserted between inner (above) and middle (below) layers. M = myostracum. Scale = 40  $\mu$ m. **G.** Outcrop pattern of CCL structure on interior surface of the whorls. Scale = 20  $\mu$ m. **H.** Vertical fracture of the same structure in inner layer. Scale = 20  $\mu$ m.





**Figure 5.** SEM micrographs of opercular microstructure of *Nerita* (*Theliostyla*) *albicilla* (UMUT RM27951). **A.** Surface of left opercular muscle scar with irregularly concentric lines. Scale = 250  $\mu$ m. **B.** Vertical fracture of outer prismatic layer. Scale = 10  $\mu$ m. **C.** Vertical fracture of the middle layer, showing spherulitic arrangement of prisms. Scale = 10  $\mu$ m. **D.** Oblique view of a section of inner prismatic layer. Scale = 5  $\mu$ m.

brown outer layer. Linear patterns of the first-order units of the middle layer are parallel near the shell margin and increase in irregularity toward the center (Figure 6). In the typical regular simple CL structure near the apertural margin, the crossing angle of the second-order lamellae is approximately 125 degrees. The inner layer consists of a CCL structure with fan-shaped second-order and lath-type third-order units (Figure 7D, E).

The inner lip projects inside along the posterior apertural margin and is formed as an extension of the CL structure of the middle layer (Figure 6). It lies between the ventral posterior of the visceral mass and the dorsal posterior of the foot of the animal.

The muscles scars are distributed in an elliptical form, keeping an almost constant distance from shell margin (Figure 6). They are inserted by two kinds of muscles of the animal: the thicker horseshoe-shaped part is the attachment of pedal retractor muscles (including head retractors in part), and the thinner anterior part is that of pallial muscle hanging the mantle onto the interior of the shell. The myostracum from these muscle scars is a thin layer of vertically oriented columnar prisms (Figure 7C). The surface of the pedal muscle scar is deeply impressed and exhibits a ridgelike

rough sculpture (Figure 7F).

**Operculum.**—The operculum is completely absent and was not found in any section of pedal musculature as already described by Sasaki (1998: 120).

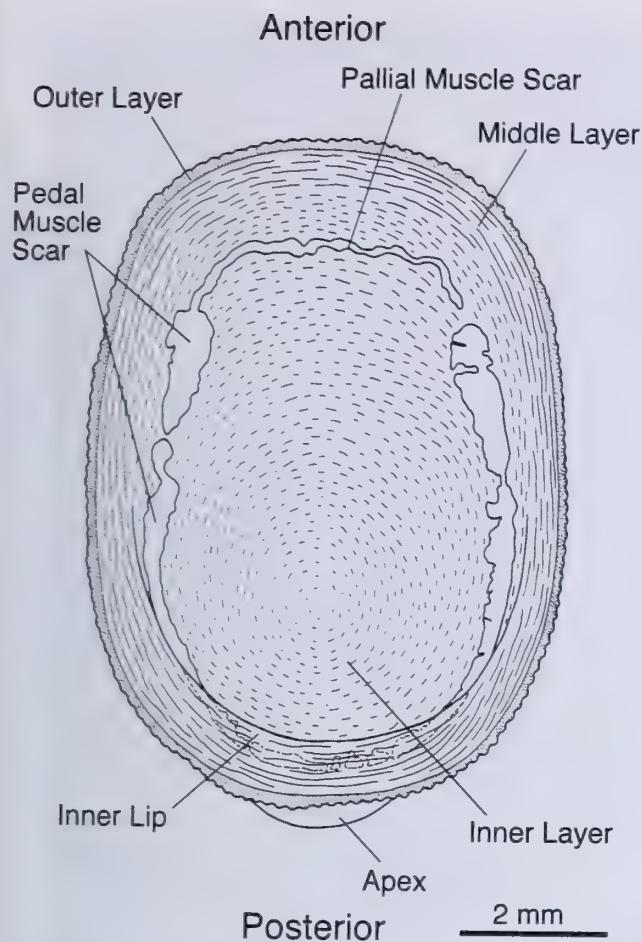
### Discussion

Recent forms of neritopsine gastropods comprise nearly 120 genera and subgenera (Vought, 1989). Although different opinions exist regarding suprageneric systematics, the Recent forms can be grouped into at least seven families, namely Neritopsidae, Hydrocenidae, Helicinidae [this family may be divided into Ceresidae, Proserpinidae, and Helicinidae (Thompson, 1980)], Titiscaniidae, Neritiliidae, Neritidae, and Phenacolepadidae ["Shinkailepadidae" is probably included here] (Ponder, 1998; Sasaki, 1998; Bandel and Fryda, 1999; Kano and Kase, 2000a, b; see also Sasaki, 1998 for their anatomical basis). Information on their shell and opercular structure can be summarized as follows.

### Shell structure of Recent Neritopsina

Shells of only ten genera belonging to six families have





**Figure 6.** Apertural view of *Cinnalepeta pulchella*. The sculpture texture of the surface is illustrated slightly schematically. The outer layer is separated from other parts by deep brown color, the middle layer is represented by concentric lines of CL structure, and the inner layer is visible as fine irregular lines of CCL structure.

been investigated at the microstructural level (Table 1). Major differences among suprageneric taxa are found mainly in the number of shell layers, the microstructure of each layer, and the crystal forms of carbonate calcium (aragonite-calcite).

(1) Neritopsidae: This family is characterized by intact inner upper whorls in contrast to other families with resorbed, hollow whorls inside (Bandel and Frýda, 1999). The shell wall of *Neritopsis radula* was described as "having two crossed-lamellar layers" by Batten (1979), but according to Suzuki *et al.* (1991), it is composed of an aragonitic outer layer of CL structure and an aragonitic inner layer of "protocrossed lamellar, irregular prismatic, homogeneous, and complex crossed lamellar structures." The mixture of four microstructures in the inner layer of *N. radula* is, therefore, a unique feature among Neritopsina.

(2) Hydrocenidae: The shell of *Georissa japonica* has three layers including the myostracum: the thicker aragonitic outer layer is of CL structure, and the thinner inner aragonitic

layer is primarily of irregular prismatic structure and subsidiarily of "protocrossed-lamellar" structure (Suzuki *et al.*, 1991).

(3) Helicinidae: The shell of *Waldemaria japonica* (Helicininae) has almost the same structural design as that of *Georissa japonica*, but the inner layer is mainly occupied by "protocrossed-lamellar" structure (Suzuki *et al.*, 1991). Microstructural data have not been provided for any other member of these families.

(4) Titiscanidae: This family totally lacks the shell at least at the adult stage (Bergh, 1890; Taki, 1955).

(5) Neritiliidae: This group had been extremely poorly known taxonomically but was redefined by Kano and Kase (2000a, b) as small neritiform gastropods with (i) spiral ridges on the protoconch, (ii) the inclination of the protoconch against the teleoconch, and (iii) perpendicular, not inclined, prisms in the outer shell layer. The shell of *Pisulina* species consists of four layers: an outer layer of simple irregular prisms, middle layer of simple CL structure, myostracum, and inner layer of CCL structure with prismatic sublayers (Kano and Kase, 2000b; figs. 6, 7).

(6) Neritidae: All neritid taxa so far investigated share a four-layered shell consisting of an outer layer of calcitic prismatic structure, middle layer of aragonitic CL structure, myostracum, and inner layer of aragonitic CCL structure (Table 1). Their shells can be further classified into two types based on relative thickness of shell layers: marine species have a thicker outer layer with a thinner periostracum, while nonmarine species have a reduced outer layer with a well developed periostracum (Suzuki *et al.*, 1991). This difference is, however, considered to be induced by environmental factors, because thin shells protected by a thick periostracum occur in various distantly related brackish and freshwater mollusks.

(7) Phenacolepadidae: The only description for this family was given for *Cinnalepeta pulchella* in this study, and the difference from other families lies in the homogeneous structure of the outer layer.

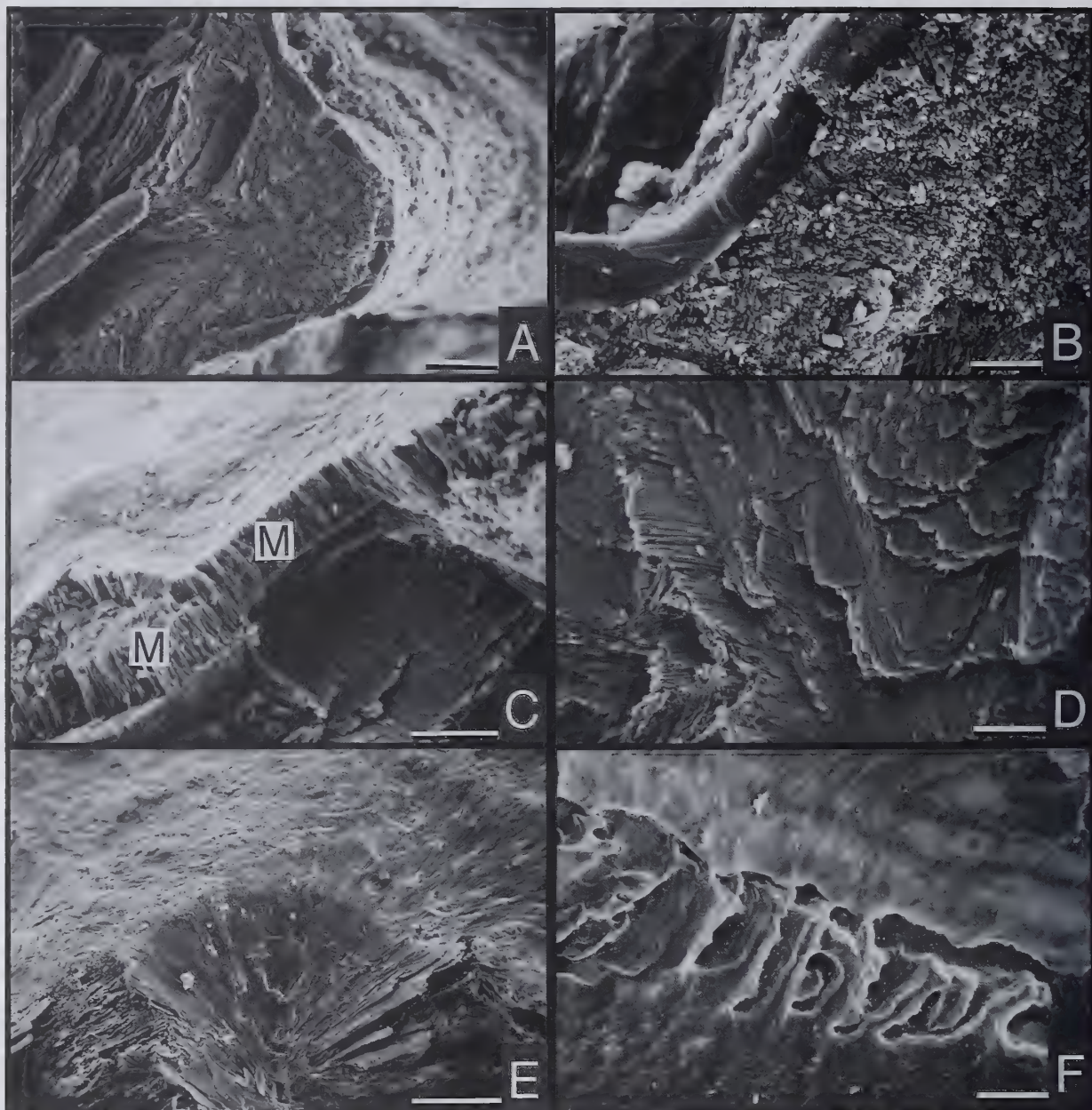
#### Operculum of Recent Neritopsina

Neritopsine operculum exhibits a great diversification in the number of calcified layers, the coverage of the organic layer, the position of calcareous layer(s) on one or both sides of the organic layer, the presence or absence of apophysis, and the morphology of muscle scars.

(1) Neritopsidae: The exterior surface of the operculum of *Neritopsis radula* is covered with a thick callus without a nucleus and spiral lines; the interior is divided into a smooth semilunar zone at the abaxial side and a large projection with a radial striation at the adaxial side (Thiele, 1929: fig. 55; Wenz, 1938: fig. 1001; Knight *et al.*, 1960: fig. 182; Ponder, 1998: fig. 15.71C, D). This projection may be the hypertrophied homologue of the apophysis of other neritopsines, with its origin shifted toward the center. The absence of a spiral line on both surfaces and a large projection from the interior center is quite unique among Gastropoda. However, no microstructural data for this family have been published to date.

(2) Hydrocenidae: The operculum of *Georissa japonica* is calcified with an apophysis and three-layered: the organic





**Figure 7.** SEM micrographs of shell microstructure of *Cinnalepeta pulchella* (UMUT RM27952). **A.** Vertical fracture of the outer layer. Scale = 20 µm. **B.** Enlarged view of homogeneous structure. Scale = 5 µm. **C.** Vertical fracture of pedal muscle scar showing the myostracum overlying the middle layer. M = myostracum. Scale = 10 µm. **D.** Vertical fracture of CCL structure near the center of the shell. Scale = 10 µm. **E.** Oblique fracture (below) and outcrop surface (above) of CCL structure. Scale = 50 µm. **F.** Oblique view of pedal muscle scar near inner lip, showing irregular rough surface. Scale = 200 µm.

layer on the outermost surface is underlain by two aragonitic layers of irregular prismatic structure (Suzuki, *et al.*, 1991: fig. 5).

(3) *Helicinidae*: This family is highly specialized for *Neritopsina* in that *Ceresinae* and *Proserpininae* completely lack an operculum, while *Helicinae* have a calcified operculum without an apophysis (Thompson, 1980). The

operculum of *Waldemaria japonica* has a single layer of calcitic blocky structure on an organic layer (Suzuki, *et al.*, 1991). *Helicinids* are strikingly different from other *neritopsines* in that calcification occurs only on the exterior surface, not interior of the organic layer.

(4) *Titiscanidae*: This shell-less taxon also lacks an operculum and is completely sluglike (Bergh, 1890; Taki,



**Table 1.** Published data on shell microstructure of the Recent Neritopsina. BL = blocky, CCL = complex crossed lamellar, CL = simple crossed lamellar, HO = homogeneous, IPR = irregular prismatic, PCL = protocrossed lamellar, PR = prismatic.

Family	Genus	Shell microstructure		Reference
		Outer layer(s)	Inner layer	
Neritopsidae	<i>Neritopsis</i>	CL	CL	Batten (1979)
	<i>Neritopsis</i>	CL	PCL, IPR, HO, CCL	Suzuki <i>et al.</i> (1991)
Hydrocenidae	<i>Georissa</i>	CL	PCL, IPR	Suzuki <i>et al.</i> (1991)
Helicinidae	<i>Waldemaria</i>	CL	PCL, IPR	Suzuki <i>et al.</i> (1991)
Neritiliidae	<i>Pisulina</i>	PR CL	CCL	Kano and Kase (2000b)
Neritidae	<i>Nerita</i>	PR CL	CCL	Bøggild (1930); Gainey and Wise (1980); This study
	<i>Nerita</i>	BL CL	PCL	Suzuki <i>et al.</i> (1991)
	<i>Neritina</i>	PR CL	CCL	Bøggild (1930)
	<i>Neritina</i>	BL CL	PCL	Suzuki <i>et al.</i> (1991)
	<i>Clithon</i>	BL CL	PCL	Suzuki <i>et al.</i> (1991)
	<i>Neripteron</i>	BL CL	PCL	Suzuki <i>et al.</i> (1991)
	<i>Septaria</i>	BL CL	PCL	Suzuki <i>et al.</i> (1991)
Phenacolepadidae	<i>Cinnalepeta</i>	HO CL	CCL	This study

1955).

(5) Neritiliidae: In the species of *Pisulina*, the operculum is secreted with exterior corneous and interior calcareous layers (Kano and Kase, 2000b: figs. 8, 9, 11). The small initial part containing the nucleus on the corneous layer is demarcated from the remaining part. The muscle scars are divided into three areas: two elongate zones along the adaxial and basal margins, and a central one extending between the nuclear zone and apophysis. The inner calcareous layers are formed of spherulitic prisms (Kano and Kase, 2000b: fig. 6F).

(6) Neritidae: The gross morphology of the neritid operculum is classified into two distinct types (see e.g. Starmühlner, 1993; Komatsu, 1986): (i) The operculum of *Septaria* (subfamily Septariinae) is embedded in the dorsal part of the foot. The anterior left corner has a sharp projection which is supposedly homologous to the apophysis of other neritopsines on the left side. (ii) The rest of the neritids (subfamilies Neritinae and Smaragdiinae) have a semilunar external operculum with a prominent apophysis.

The opercular microstructure of neritids is known to be variable, depending on habitats. The marine neritids have a common opercular plan with a single exterior aragonitic prismatic layer, an organic layer, and two interior aragonitic prismatic layers (Suzuki *et al.*, 1991: fig. 5; this study: Figs. 4, 5). The opercula of nonmarine species (*Neritina* and *Clithon*) have only two aragonitic prismatic layers covered by a well developed organic layer (Suzuki *et al.*, 1991).

The operculum of *Bathynnerita naticoidea* (tentatively treated as a neritid here) dwelling exclusively in deep-sea hydrocarbon seeps is "partly calcified with a thicker calcareous layer where it is attached to the foot" (Warén and Bouchet, 1993), and the apophysis is absent. Its operculum with only partial calcification is greatly different from those of shallow-water neritids.

(7) Phenacolepadidae: The opercular morphology of phenacolepadids can be divided into three distinct states. (i) The presence of a vestigial internal operculum with inte-

rior calcification and rudimentary apophysis was documented by Fretter (1984) in *Phenacolepas omanensis* and observed with SEM for the first time by Kimura and Kimura (1999: fig. 7C, D) in *Phenacolepas* sp. (ii) The opercula of so-called "Shinkailepedidae" has double structure of calcified anterior and noncalcified posterior parts as described in *Shinkailepas* by Okutani *et al.* (1989: fig. 12) and Beck (1992: pl. 1, fig. 4) and in *Olgasolaris* by Beck (1992: pl. 5, fig. 4). Double-layered nail-shaped operculum is strikingly convergent with that of the neritid genus *Septaria*. (iii) The operculum is absent in *Cinnalepeta*, as described above.

#### Implication of neritopsine hard-part microstructures

It has been generally accepted that microstructural characters of the shells are useful for the understanding of molluscan higher taxonomy. It is, however, necessary to check the correlation between taxonomic distribution of structural morphotype and phylogenetic relationships in the Recent taxa before comparing extant and extinct forms directly.

(1) Shell structure: As reviewed above, the patterns of shell structure of the Recent Neritopsina can be categorized into two major types: (i) Genera of three families, Neritidae, Phenacolepadidae, and Neritiliidae, all have four-layered shells in which inner CCL and middle CL layers are overlaid by a prismatic (in Neritidae and Neritiliidae) or homogeneous (in Phenacolepadidae) shell layer. (ii) By contrast, other families such as Neritopsidae, Helicinidae, and Hydrocenidae secrete three-layered shells which consist mostly of CL/CCL structures and lack an additional outer layer. This apparent difference between the two groups may be viewed as expressing the distinctness of their relationship, but it is still premature to present phylogenetic implication because of the lack of a reliable phylogenetic hypothesis. The phylogenetic analysis has been conducted only in a part of Neritopsina by Holthuis (1995) and Sasaki (1998), and the phylogenetic status of Neritopsidae, Helicinidae, and Hydrocenidae is totally unknown. The scarceness of struc-



tural data relative to the number of existing genera is also problematic so far as testing the stability of character states within each family.

Another unresolved problem is whether all of the taxa with a four-layered shell share a calcitic outer layer or not. Suzuki *et al.* (1991) revealed that at least the shell of neritids is constructed from a calcitic outer layer and otherwise aragonitic layers in contrast to the entirely aragonitic shell of other families. They argued that this bimineralic composition is attributable to adaptation to a shallow aquatic environment, probably as a means of reinforcing the mechanical strength of the shell. Thus, it should be tested as a next step whether non-neritid four-layered shells are also made of two crystal forms of calcium carbonate. Concerning the outermost shell layer, Taylor and Reid (1990) revealed the parallel homoplastic addition of a calcitic outer layer in some genera within littorinid gastropods. This means that the convergence in conchological characters should necessarily be considered also at the microstructural level in other groups of molluscs.

(2) Opercular structure: The opercular structure can be divided into several types as a result of the above comparison: (i) three (single exterior and two interior) aragonitic layers in marine neritids, (ii) two interior aragonitic layers in Hydrocenidae and nonmarine neritids, (iii) single calcitic exterior layer without interior calcification in Helicininae, (iv) interiorly calcified operculum with unknown layer distribution in Neritiliidae and a part of Phenacolepadidae, and (v) absence of an operculum in Titiscaniidae and in part in the Phenacolepadidae and Helicinidae. Thus, a single similar state often occurs across several different families, and also several different states can coexist within the same family. At the family level the similarity and dissimilarity in opercular structure are very difficult to explain in the phylogenetic context.

In connection with nonphylogenetic factors, the less calcified opercula in nonmarine neritids as compared with marine confamilial members may be explained as a consequence of adaptation to low-salinity environments (Suzuki *et al.*, 1991). However, in other taxa, there is no clear correlation between opercular structure and habitat selection. The marked differences in neritopsine opercular structure is difficult to understand also in terms of adaptation. The possession of apophysis is presumably under phylogenetic control within Neritopsina, and at the same time, it is a convergent state also found in caenogastropod rissoideans. The peglike structure has possibly arisen to increase the area of muscular attachment in this case.

Because of the insufficient resolution of neritopsine phylogeny and the lack of mineralogical data in part, the evolutionary scenario of neritopsine hard parts remains largely speculative at present. For further studies, exoskeletal structure including mineralogical characters should be investigated more comprehensively in whole extant and extinct neritopsines together with the comparative anatomy and molecular phylogeny of the Recent species.

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## Geometric pattern and growth rate of prismatic shell structures in Bivalvia

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**Abstract.** The distribution patterns, sizes and nucleation sites of aggregated prisms on the outer shell surface were examined in 16 species of Bivalvia and modeled theoretically. Biometric analysis shows a negative correlation between the median size and variation of sizes of calcitic simple prisms. In species with aragonitic vertical composite prisms, instead, the density of prisms tends to decrease when their nucleation sites are randomly distributed. Comparison of the results of computer simulations with those of biometric analyses reveals the following: 1) a positive correlation between growth rate of prisms and the probability of nucleation for simple prisms, and 2) a limit of the number of nucleations per unit time in vertical composite prisms. Prism size correlates with the growth rate of the entire shell or prisms, and increases as the shell grows faster or prisms grow slower.

**Key words:** biomineralization, bivalves, prismatic structure, shell growth rate, theoretical morphology

### Introduction

The microscopic features of a molluscan shell record certain physiological conditions of the organism at the time the shell is formed. Carbonate minerals within a molluscan shell crystallize and grow under physicochemical conditions controlled by the physiology of the organism. Wada (1972, 1985) reported a seasonal change of shape and size of aragonite crystals in the nacreous layer of such bivalves as *Pinctada fucata*, *Pinna attenuata* and *Hyriopsis schlegeli*. He suggested that the topography of growing crystals may reflect the rate of crystal growth or the degree of supersaturation of the extrapallial fluid. Quantitative analysis of the relationship between size and/or shape of crystals and the rate of crystal growth within a shell provides a reliable basis to understand the 'paleophysiology' of fossil organisms.

The goal of this study is to clarify the relationship between the geometry of bivalve shell microstructure and the relative growth rate of crystals or of the entire shell. For this purpose, the present study focuses on the geometry of the outer shell surface of a simple or vertical composite prismatic shell layer. Although they differ in the ultrastructure of prisms, those two prismatic structures both consist of many parallel-arrayed columnar units (Carter and Clark, 1985; Carter *et al.*, 1990). Each prism is surrounded and bounded by an organic matrix showing a honeycomb-like appearance on the outer shell surface.

For understanding the rule or algorithm forming the geometric pattern of shell microstructure, theoretical morphology is particularly useful (Ubukata, 1997a, b, 2000). In the present study, a biometric analysis of size and nucleation sites of prisms in actual shells was carried out in 16 species. Furthermore, a theoretical morphological modeling of growth kinematics of aggregated prisms was attempted, and the computer simulations of that model were compared with the results of the biometric analyses.

### Biometric analyses

#### Material and methods

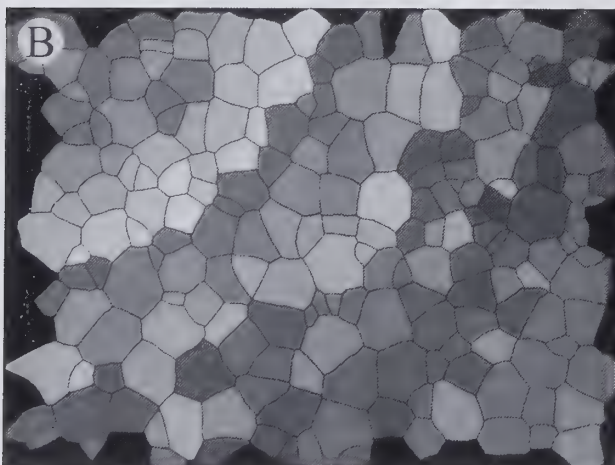
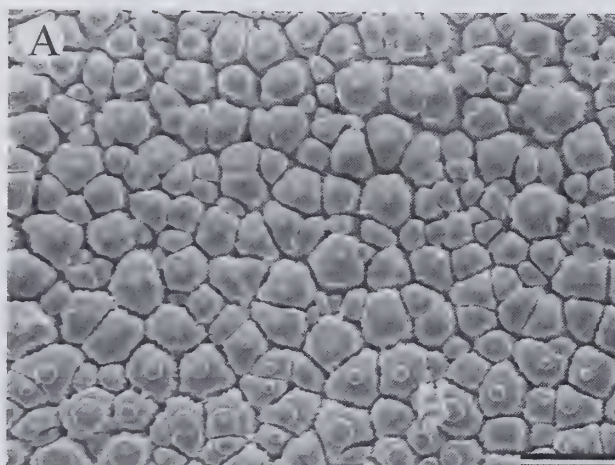
The outer shell surface of a simple prismatic or vertical composite prismatic outer shell layer was examined in 16 extant species of Bivalvia (Table 1). Each species was represented by a single specimen, except *Anodonta woodiana*. Most of them were collected at various localities around the Japanese Islands and the Philippines. All the specimens examined are stored at Shizuoka University (SUM).

In order to remove the periostracum from the shell completely, the shells examined were bleached for one day. Pieces of them were washed, dried in air, coated with gold using a JEOL JFC-1500 ion coater, and examined with a JEOL JSM-5800LV scanning electron microscope operated at 15kV and interfaced to a computer (Dell Optiplex Gxa EM).

In order to analyze size-frequency distribution of prisms,

**Table 1.** List of material examined. All specimens have the prefix SUM.

Family	species	locality	specimens
Pteriidae	<i>Pteria penguin</i> (Roding)	San Luice, Bathangas, Philippines	HM-B-0014
	<i>Pinctada maculata</i> (Gould)	Iriomote Is., Okinawa, southwest Japan	HM-B-0015
Isognomonidae	<i>Isognomon perna</i> (Linnaeus)	Iriomote Is., Okinawa, southwest Japan	HM-B-0016
	<i>I. ephippium</i> (Linnaeus)	San Luice, Bathangas, Philippines	HM-B-0017
Malleidae	<i>Malleus regula</i> (Forskål)	Iriomote Is., Okinawa, southwest Japan	HM-B-0018
Pinnidae	<i>Atrina pectinata</i> (Linnaeus)	Ariake, Saga, western Japan	HM-B-0019
	<i>A. vexillum</i> (Born)	Honda Bay, Palawan, Philippines	HM-B-0020
Ostreidae	<i>Crassostrea gigas</i> (Thunberg)	Misaki, Kanagawa, Central Japan	HM-B-0021
Margaritiferidae	<i>Margaritifera laevis</i> (Haas)	Nakagawa, Hokkaido, northern Japan	HM-B-0022
Unionidae	<i>Inversidens reiniana</i> (Kobelt)	Lake Biwa, Shiga, Central Japan	HM-B-0023
	<i>Unio biwae</i> Kobelt	Lake Biwa, Shiga, Central Japan	HM-B-0024
	<i>Lanceolaria oxyrhyncha</i> (Martens)	Lake Biwa, Shiga, Central Japan	HM-B-0025
	<i>Anodonta woodiana</i> (Lea)	Lake Biwa, Shiga, Central Japan	HM-B-0026, -0027
	<i>A. calyptygus</i> Kobelt	Lake Biwa, Shiga, Central Japan	HM-B-0028
	<i>Cristaria plicata</i> (Leach)	Lake Biwa, Shiga, Central Japan	HM-B-0029
Trigoniidae	<i>Neotrigonia margaritacea</i> (Lamarck)	French Is., Australia	HM-B-0030



areas of prisms on the outer shell surface were measured at 6–12 positions along a growth increment on the shell surface. An SEM image of the measured portion was saved as a computer bitmap file (Figure 1A). Next, the boundaries between prisms were traced on a NEC PC-9821 V166 personal computer using Microsoft PowerPoint 7.0, and then each prism was colored differently using Justsystem Hanako PhotoRetouch (Figure 1B). Subsequently, the area of each prism was measured by counting pixels. For this counting, a program written in VISUAL BASIC was used on a personal computer.

Since the size-frequency distribution of the areas of prisms is generally right-skewed, the mean and standard deviation are not suitable for representing the distribution of the areas of prisms. Therefore, the “average” area of prisms on a shell is represented by the median of the areas ( $\tilde{S}$ ), and the variation of the areas is expressed as a standardized hinge spread ( $Q_s$ ), which is defined as follows:

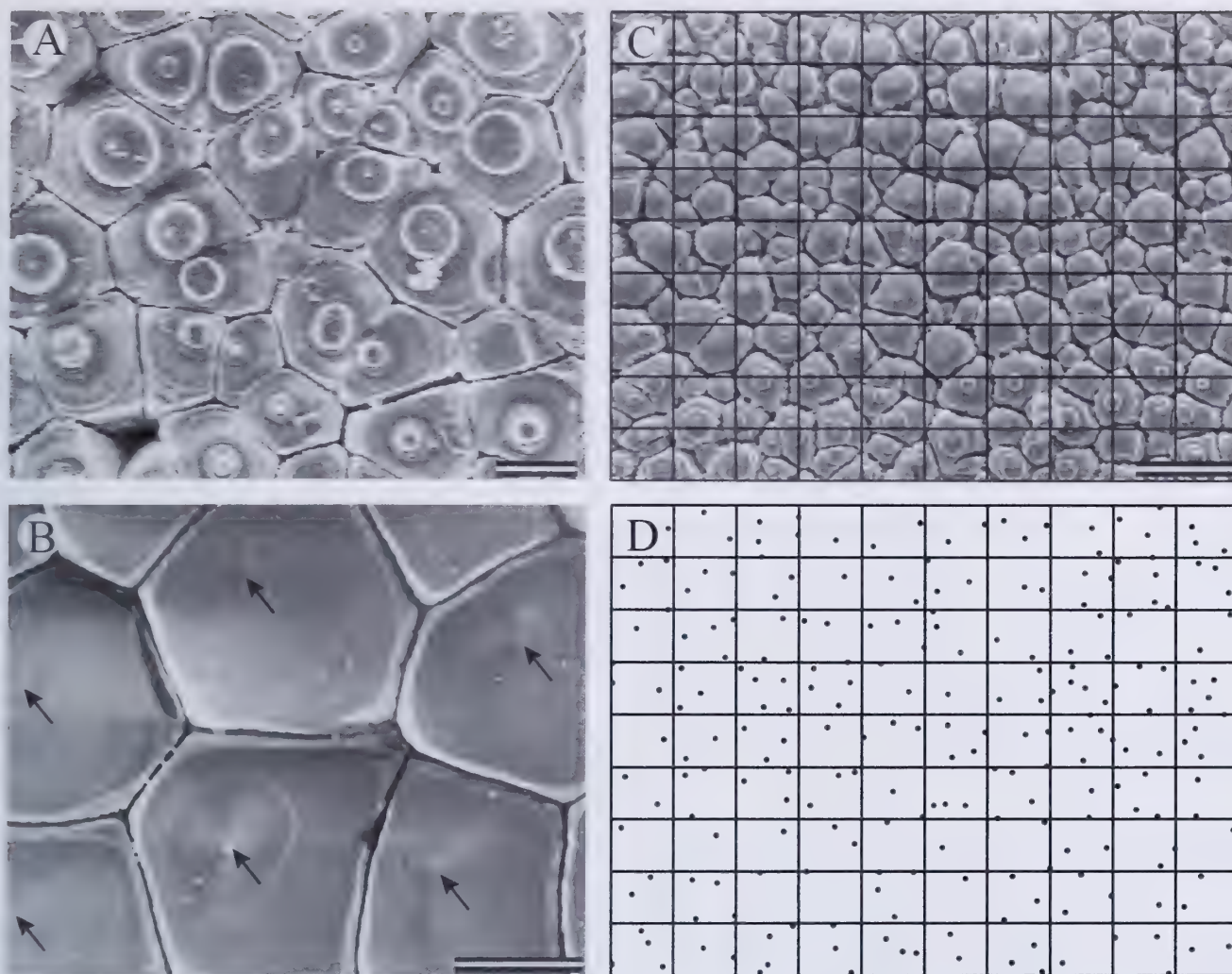
$$Q_s = \frac{Q_3 - Q_1}{\tilde{S}}, \quad (1)$$

where  $Q_1$  and  $Q_3$  are the first and third quartiles of the areas of prisms, respectively (Hoel, 1976).  $\tilde{S}$  and  $Q_s$  were both estimated in all shell portions examined.

On the outer surface of a vertical composite prismatic shell layer, microgrowth increments are clearly visible within a bleached prism (Figure 2A). In a simple prismatic shell layer, growth increments within a prism are faintly observed on the bleached shell surface (Figure 2B). In either case,

**Figure 1.** A. SEM photograph of the outer shell surface of the vertical composite prismatic layer in *Anodonta woodiana* (SUM-HM-B0027), scale: 50  $\mu$ m. B. Trace of the outlines of prisms on the SEM image of A.





**Figure 2.** A. SEM photograph of the outer shell surface of the vertical composite prismatic shell layer in *A. woodiana* (SUM-HM-B0027) showing clear growth increments within individual prisms, scale: 20  $\mu$ m. B. The simple prismatic layer in *Pinctada maculata* (SUM-HM-B0015). Arrows indicate nucleation sites, scale: 20  $\mu$ m. C. The SEM image of *A. woodiana* subdivided into squares, scale: 50  $\mu$ m. D. Distribution of nucleation sites of prisms in C.

the center of the circular growth increments is regarded as the nucleation site of the prism.

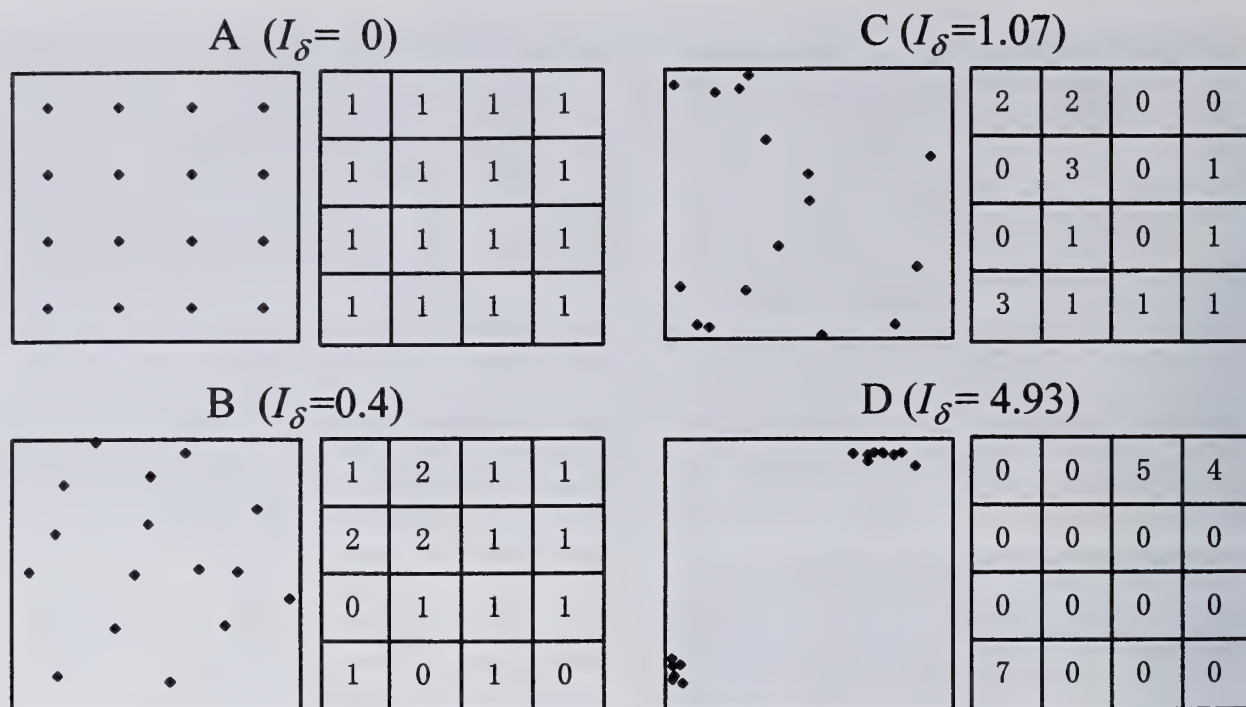
The distribution of nucleation sites of prisms was analyzed in all shell portions in which the areas of prisms were measured. An SEM image was divided into a squared grid of appropriate size for each square to include an average of two nucleation sites (Figure 2C). Next, the number of nucleation sites was counted in each square (Figure 2D). The numbers of squares and nucleation sites in each square both define the  $I_s$  index of Morisita (1959), which represents the nonuniformity of a distribution independent of the size of the quadrates. The  $I_s$  index is defined as:

$$I_s = \frac{n \sum x_i(x_i - 1)}{\sum x_i (\sum x_i - 1)} \quad (2)$$

where  $n$  is the number of squares,  $x_i$  is the number of sites in the square  $i$ . The value of  $I_s$  is zero when the distribution is perfectly uniform (Figure 3A).  $I_s$  increases as the distribution becomes nonuniform (Figure 3B), and it is expected to be one when sites are distributed randomly (Figure 3C). When the distribution of sites is biased considerably,  $I_s$  has a large value (Figure 3D). The value of  $I_s$  was estimated in every shell position examined, and the nonuniformity of the distribution of nucleation sites was represented by  $I_s$ .

### Results

The biometric analyses revealed a negative correlation between  $\bar{S}$  and  $Q$ , in a single specimen of *Isognomon perna*, and a positive correlation in a single specimen of *Malleus regula* (Figure 4B). In another species, no correlation was observed, though the number of measured portions



**Figure 3.** Effect of the spatial distribution pattern on the value of  $I_s$ . In this figure, the area is divided into 16 contiguous squares each including a number of or no dots. **A.** Perfectly uniform distribution. **B.** Nearly uniform distribution. **C.** Random distribution. **D.** Considerably concentrated distribution.

within a single valve was not large enough to be significant. On the other hand, when the data from all species are combined,  $Q_s$  is negatively correlated with  $\bar{S}$  at the 0.01 level of significance, both for simple prismatic and vertical composite prismatic shells (Figure 4A–B). This shows that variation in the size of prisms tends to decrease as prism size increases. The negative correlation between  $Q_s$  and  $\bar{S}$  is clear especially in species with a simple prisms (Figure 4B), while the correlation is more or less obscure in species with vertical composite prisms (Figure 4A).

A positive correlation between  $I_s$  and  $Q_s$  is found only in each specimen of *Unio biwae*, *Anodonta woodiana* and *Malleus regula* (Figure 4C, D). However, when all the data are combined, a positive correlation clearly emerges between  $I_s$  and  $Q_s$  in species with vertical composite prisms (Figure 4C). In the case of species with simple prisms,  $Q_s$  is positively correlated with  $I_s$  at the 0.05 level of significance, though the correlation is graphically unclear (Figure 4D). The positive relationship between  $I_s$  and  $Q_s$  indicates that variation of the size of prisms tends to increase with increasing randomness of the distribution of nucleation sites.

### Theoretical morphology

#### Growing circles model

To better understand the relationships between geometric features of prisms and the growth rate of each prism and/or of the net growth rate of the entire shell, the growth of aggregated prisms was modeled theoretically.

For modeling the process of microscopic growth, observing the initial growth stage of prisms helps understand the nature of crystal growth. Formerly, I reported that many small hemispherical incipient prisms occur on the inner surface of the periostracum at the growing margin in species possessing simple and vertical composite prisms (Ubukata, 1994, pl. 2, figs. 1–3). Consequently, a growing-circles model, which represents the growth of aggregated prisms, is introduced here.

Growth of a prismatic shell layer consists of three elements, namely, nucleation of prisms, growth of prisms, and accretionary growth of the entire shell. During a single short growth step, the mantle secretes calcium carbonate and nucleation of prisms occurs within the nucleation zone on the inner surface of a periostracum (Figure 5A). The periostracum subsequently secreted by the mantle edge pushes the earlier produced periostracum and its incipient prisms into a more proximal part of the shell (Saleuddin and Petit, 1983). After the prisms pass through the nucleation zone, prisms gradually grow and elongate, forming a columnar structure.

Let us consider hypothetical shell growth (Figure 5B). The accretionary growth of the entire shell during a short period of time is reflected in a shift of the nucleation zone. Growth of a prism is represented by the kinematics of an enlarging circle. Potential nucleation sites are distributed uniformly within a nucleation zone of width  $h$ . The distance between the potential nucleation sites can be expressed by  $d$ , which represents the size of a unit cell. Growth compo-



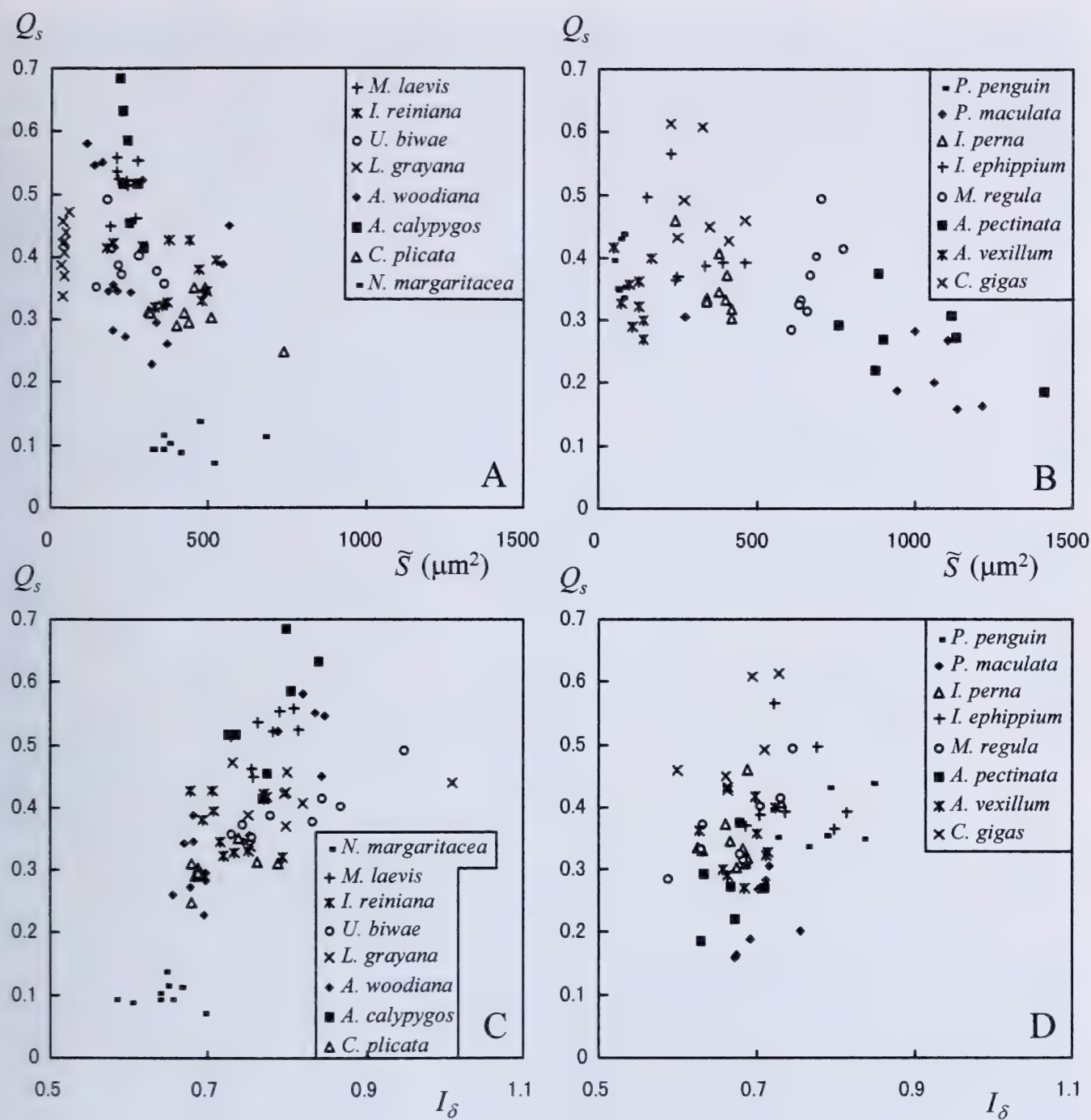
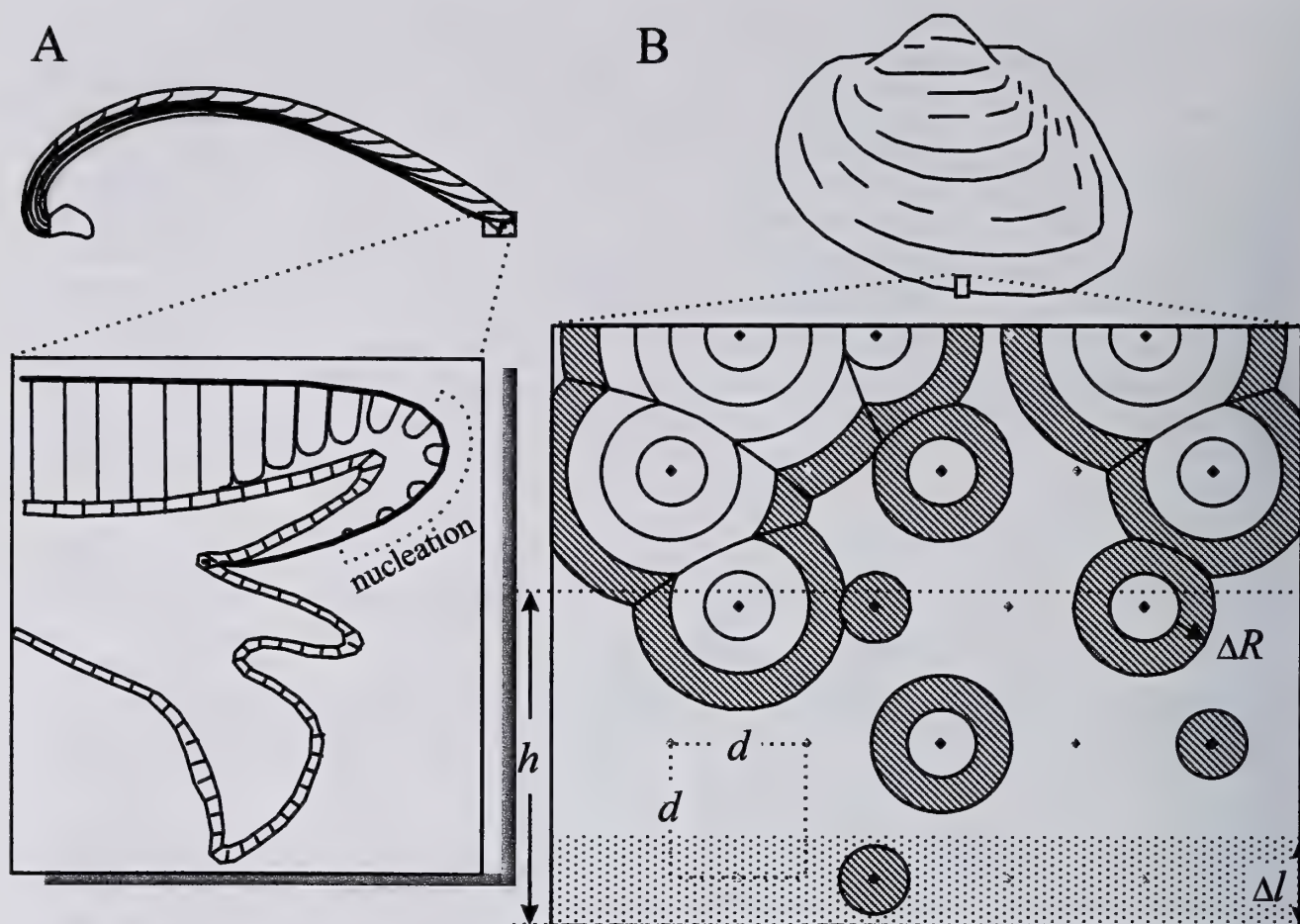


Figure 4. A-B. Relationship between  $\tilde{S}$  and  $Q_s$  in actual shells. A. Data from species with vertical composite prisms. B. Data from species with simple prisms. C-D. Relationship between  $I_\delta$  and  $Q_s$  for species with vertical composite prisms (C) and simple prisms (D).

nents are expressed as functions of growth stage  $s$ , rather than as functions of time, since the time scale of the growth process is difficult to ascertain in many cases. Over a period of one growth step, the mantle secretes a periostracum at the shell margin, giving rise to the stippled area in Figure 5B. If the growing margin of the shell shifts downward by  $d$

during the step, the growth step is regarded to be a unit interval of the growth. Then, the growth step  $\Delta s$  is generally defined as:

$$\Delta s \equiv \frac{\Delta l}{d}, \quad (3)$$



**Figure 5.** **A.** Schematic diagram of the radial section of the shell and mantle margin of a bivalve showing the position where nucleation of prisms occurs. **B.** The growing circles model. Black bold points indicate initiation sites of produced prisms, and gray ones potential nucleation sites of unborn prisms. During a given growth step  $\Delta s$ , the shell margin shifts by  $\Delta l$  (stippled area) and the radius of prisms increases by  $\Delta R$  (shaded area). The dotted line indicates the dorsal limit of the nucleation zone.

where the growing margin of the shell shifts by  $\Delta l$  during the growth step.

Meanwhile, nucleation of a prism occurs at a potential nucleation site within the nucleation zone with a probability of  $q$ . Each prism is approximated by a circle which enlarges at a steady rate. During a growth step  $\Delta s$ , calcium carbonate precipitates along the circumference of each prism giving rise to a new additional rim shown by the shaded portion in Figure 5B, and the radius of each circle increases by  $\Delta R$ . As the prisms grow, neighboring prisms come closer and finally in contact with one another, as a result forming a boundary between two prisms. Nucleation of prisms occurs randomly during each growth step, as a result of irregularity of the settling time among prisms. Consequently, a growing circle often occupies the space of nucleation and/or growth of a neighboring 'unborn' prism. A newborn prism sometimes loses in competition for space between neighboring prisms, and is geometrically terminated (Grigor'ev, 1965).

In the growing-circles model, growth of a shell and prisms is generally expressed by the following three parameters:  $C$

: the standardized growth rate of prisms, defined as the increase of the radius of a prism per growth step, normalized by size of a unit cell ( $d$ ),  $P$ : probability of nucleation per growth step in each potential site, and  $L$ : the extent of the nucleation zone standardized by  $d$ . Probability of 'failure' of nucleation at each site per growth step is expressed as  $1-P$ , and the probability of failure of nucleation during a growth step  $\Delta s$  ( $=1-q$ ) is obtained by raising  $1-P$  to  $\Delta s^{\text{th}}$  power. Then, three growth parameters  $C$ ,  $P$  and  $L$  are given by:

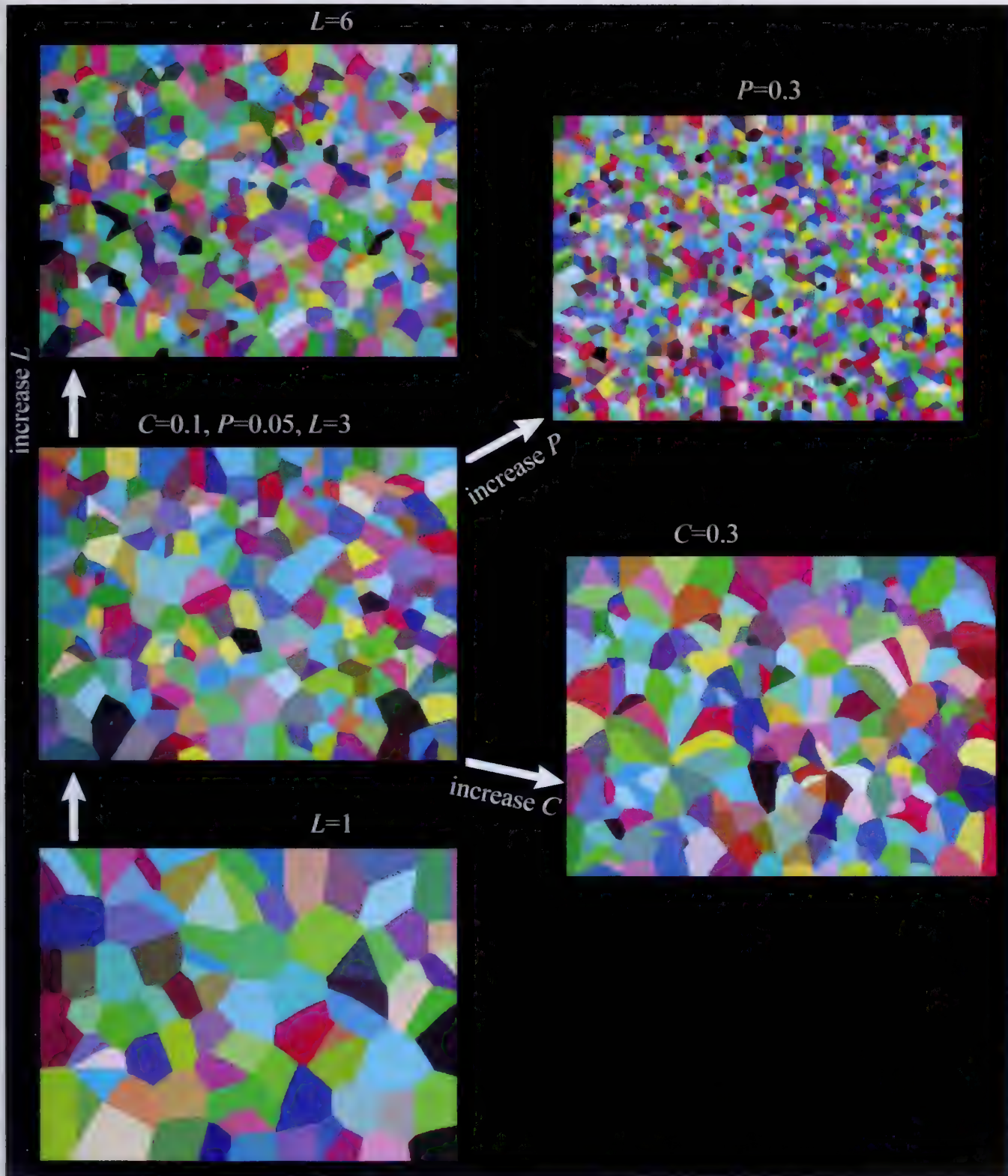
$$C \equiv \frac{\Delta R}{\Delta l}, P \equiv 1 - (1 - q)^{\frac{1}{\Delta s}}, L \equiv \frac{h}{d}. \quad (4)$$

Now, we can generally define a growth increment during an arbitrary growth step if three parameters  $C$ ,  $P$  and  $L$  are given.

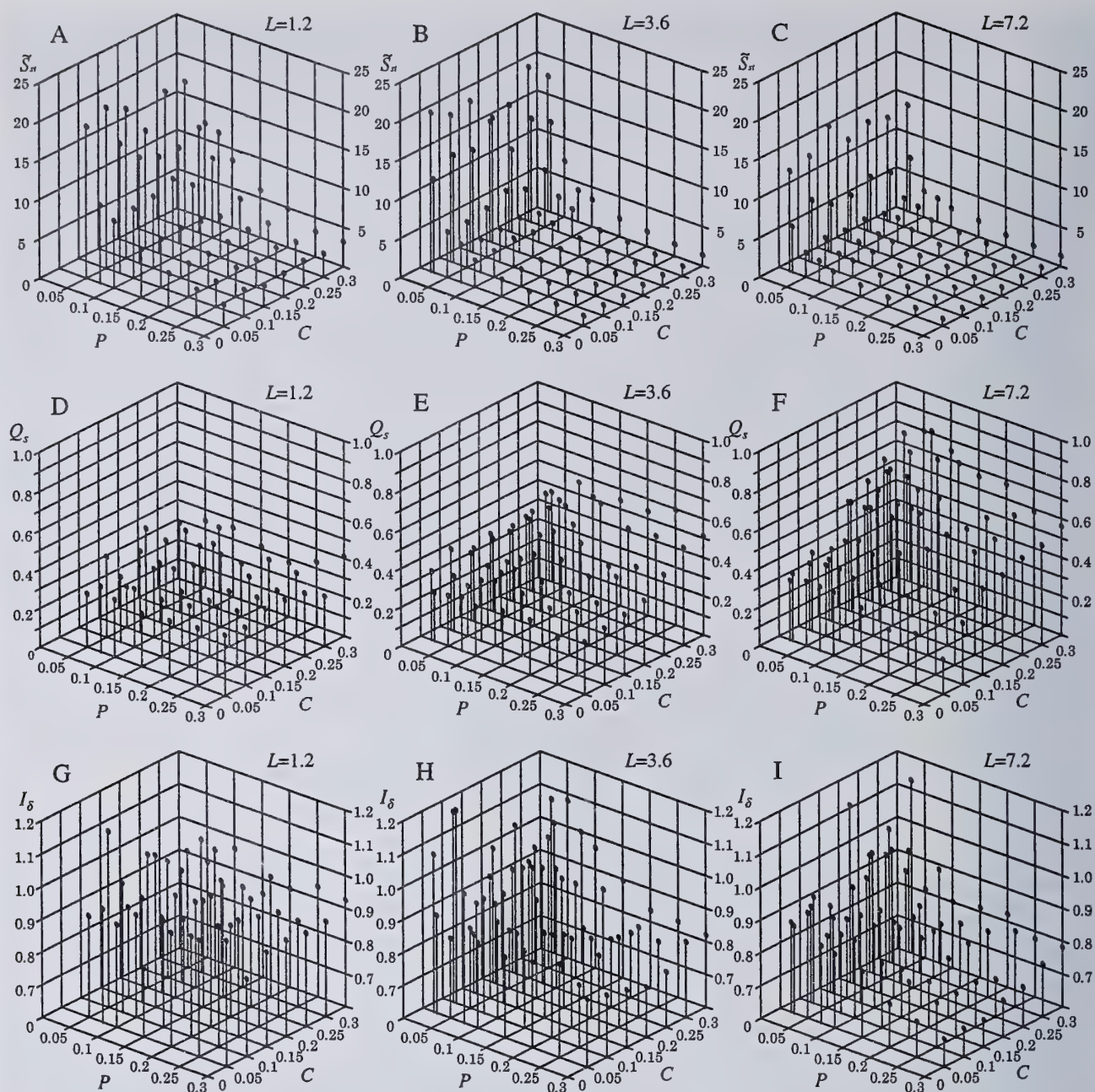
#### Computer simulation

In order to evaluate the effects of parameters  $C$ ,  $P$  and  $L$  on the geometric pattern of prismatic structure, computer simulations were performed for growth of prisms based on





**Figure 6.** Color display of the growing circles model. Each prism is identified by its color. As  $C$  increases, size variation of the prisms also increases. As  $P$  or  $L$  increases, the median size of prisms tends to decrease.



**Figure 7.** Three-dimensional block diagrams showing the relationships among growth parameters ( $C$ ,  $P$ ,  $L$ ) and statistics  $\bar{S}$  (A-C),  $Q_s$  (D-F) or  $I_\delta$  (G-I) on a  $C$ - $P$  diagram at  $L$  values of 1.2, 3.6 and 7.2.

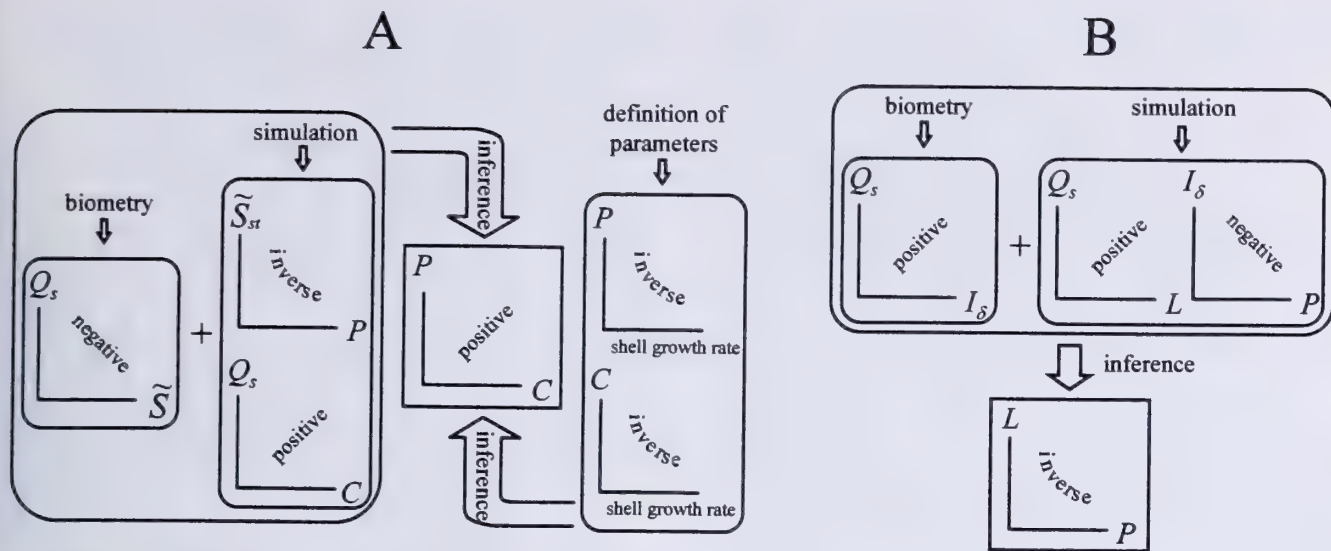
the growing-circles model. In the theoretical model, the area of a hypothetical prism was measured as the number of pixels ( $A$ ) on the display surface, and both the standardized hinge spread ( $Q_s$ ) and the median of a standardized area of hypothetical prisms ( $\bar{S}_v$ ) defined below were estimated in each model:

$$\bar{S}_v \equiv \frac{\bar{A}}{d^2}, \quad (5)$$

where  $\bar{A}$  is the median of  $A$ . The dimension of  $d$  is expressed as pixels on the computer. The coordinates of a nucleation site were recorded on each hypothetical prism for calculating the value of  $I_\delta$  in a model. Computer simulations were carried out with a program written in VISUAL BASIC by means of a 64-bit workstation computer (Visual Technology VT-Alpha 600) interfaced with a CRT (Iiyama A702H).

Figure 6 shows a spectrum of geometric patterns of hypothetical prisms that were made by the growing circles model.





**Figure 8.** Summary of the biometric analyses and computer simulation. From coupling their results with the consequences from definition of the parameters, a relationship between growth parameters is inferred either in simple prisms (A) or composite prisms (B).

Each prism is identified by its color in a theoretical prismatic structure. If  $C$  is large, each prism grows considerably while it passes through the nucleation zone, as a result of the great irregularity of the birth time among prisms. Then, as  $C$  increases, the variation of prism size also increases. As  $P$  or  $L$  increases, the number of prisms increases while their size decreases.

Three-dimensional scatter diagrams illustrating the values of  $\tilde{S}_n$  in relation to  $C$  and  $P$ , at  $L=1.2, 3.6$  and  $7.2$  are given in Figure 7A–C, respectively.  $\tilde{S}_n$ , which means an 'average' prism size, seems to be inversely proportional to  $P$ , which represents the probability of nucleation. In addition, at the same combination of  $C$  and  $P$ ,  $\tilde{S}_n$  tends to increase as  $L$  decreases. This fact indicates that the size of hypothetical prisms increases as the nucleation zone becomes narrow.

Figure 7D–F is a series of diagrams showing the relationship among four parameters  $C, P, Q$ , and  $L$ . When  $L$  is large enough,  $Q$  is positively correlated with  $C$  (Figure 7E, F). This fact suggests that variation of prism size tends to increase with increasing growth rate of prisms ( $\Delta R$  in Eq.1) or with decreasing the accretion rate of the entire shell ( $\Delta l$  in Eq.1). When  $L$  is small, no clear relationship exists between pairs of  $C, P$  and  $Q$ . (Figure 7D). In a high  $C$  condition,  $Q$ , at a given  $P$  also tends to increase with increasing  $L$  (Figure 7D–F).

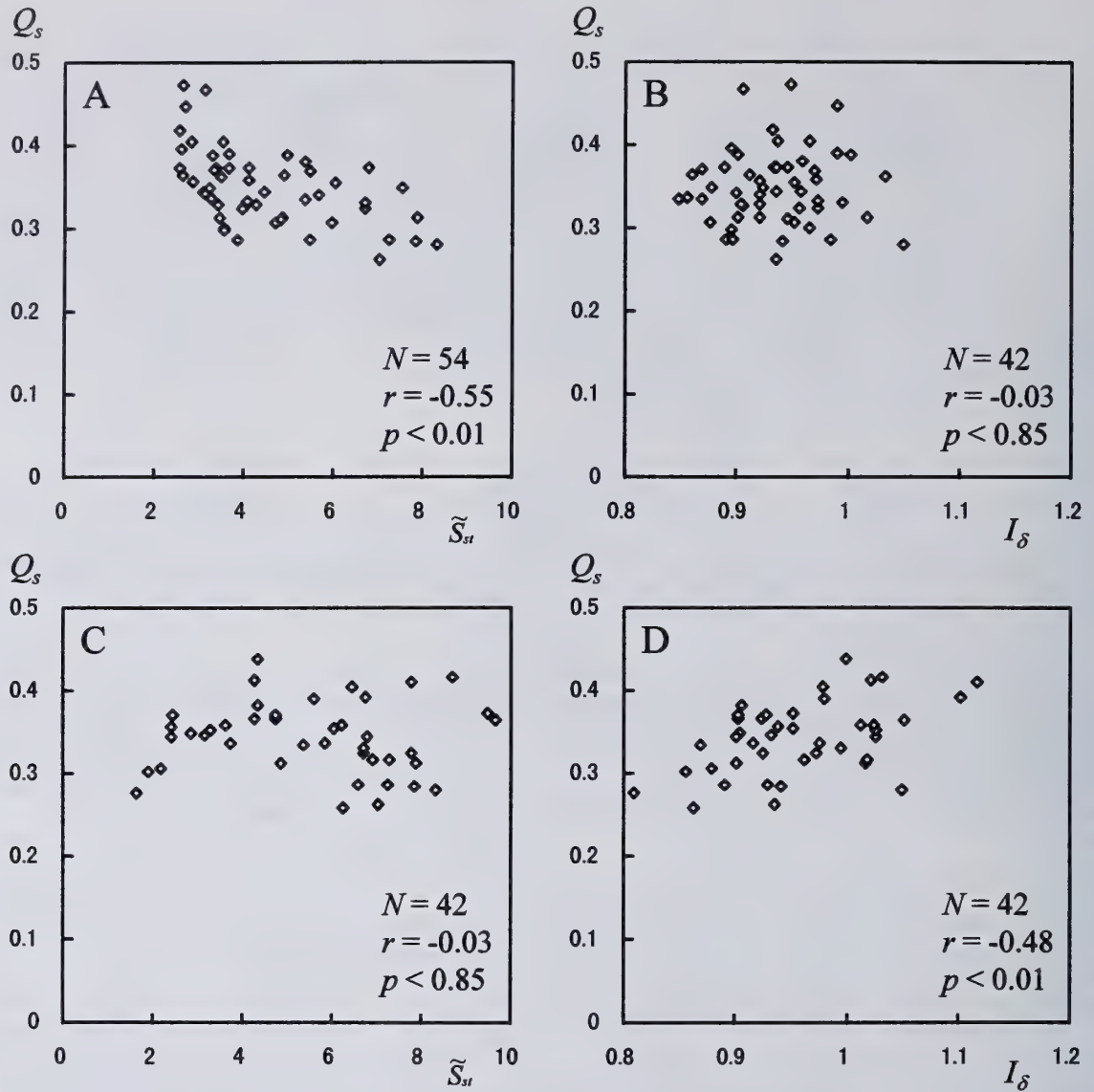
Figure 7G–I shows the variation of  $I_\delta$  in relation to  $C, P$  and  $L$ . When  $L$  is large,  $I_\delta$  gradually decreases with increasing  $P$ . Since  $I_\delta$  represents the degree of nonuniformity, this result indicates that the nucleation sites tend to be distributed uniformly as the probability of nucleation increases. In the high  $P$  region,  $I_\delta$  at a given  $C$  decreases as  $L$  increases. This fact indicates that nucleation sites tend to be distributed randomly as the nucleation zone becomes narrower, when the probability of nucleation is high enough.

#### Geometric pattern and growth rate of prismatic shell

As mentioned above, the biometric analyses indicated a negative correlation between  $\tilde{S}$  and  $Q$ , especially in the species with simple prisms (Figure 4B), and the computer simulation predicted an inverse relationship between  $P$  and  $\tilde{S}_n$  (Figure 7A–C) and also a positive correlation between  $C$  and  $Q$ . (Figure 7E, F). To sum up these results, it can be predicted that  $P$  increases as  $C$  increases for those species with simple prisms (Figure 8A). That is also inferred from the definition of parameters. Since both  $P$  and  $C$  are inversely proportional to the growth rate of the entire shell, a positive correlation between  $C$  and  $P$  is quite reasonable (Figure 8A) if the size-frequency distribution of prisms is controlled mainly by the growth rate of the entire shell. Furthermore, even if both the growth rate of prisms and the probability of nucleation reflect the activity of mantle secretion, and if the size of prisms is controlled mainly by the activity of mantle secretion, the positive correlation between  $C$  and  $P$  is also expected.

Coupling of the biometrics and the simulation also suggests to us a relationship between the parameters  $P$  and  $L$ . The biometric analyses demonstrated a positive correlation between  $I_\delta$  and  $Q$ , especially for species with vertical composite prisms as shown in Figure 4C. In addition, the computer simulation predicted a positive relationship between  $L$  and  $Q$ , and a negative correlation between  $P$  and  $I_\delta$  as shown in Figure 7G–I. These two results suggest that  $P$  possibly decreases as  $L$  increases in species with vertical composite prisms (Figure 8B). Actually, an inverse relationship between  $L$  and  $P$  is expected if we assume that the frequency of nucleation per unit time interval is fixed.

To ascertain this prediction, relationships among simulated values of  $\tilde{S}_n, I_\delta$  and  $Q$  were analyzed for each combina-



**Figure 9.** Relationships between  $\tilde{S}_{st}$  and  $Q_s$  and between  $I_\delta$  and  $Q_s$  when three parameters satisfy equations as follows:  $C=aP$ ,  $P=b/L$ , where  $a$  and  $b$  are coefficients.  $N$  represents the total number of samples examined,  $r$  exhibits the correlation coefficient, and  $p$  is the significance level of the correlation. **A–B.**  $a=3$ ,  $0.05 \leq b \leq 0.175$ . **C–D.**  $1 \leq a \leq 3$ ,  $b=0.05$ .

tion of  $C$ ,  $P$  and  $L$ , when a positive correlation between  $C$  and  $P$  and an inverse relationship between  $L$  and  $P$  are assumed, as in the following relations:

$$C = aP, \quad P = \frac{b}{L}, \quad (6)$$

where  $a$  and  $b$  are coefficients. Computer simulations were performed under the following conditions: 1)  $a$  is fixed to 3, and  $b$  varies between 0.05 and 0.175, 2)  $a$  varies between 1 and 3, and  $b$  is fixed to 0.05. Figure 9 is a diagram showing the relationships between  $\tilde{S}_{st}$  and  $Q_s$  and between  $I_\delta$  and  $Q_s$ .

The results of the simulations under a fixed value of  $a$  ( $=3$ ) and various values of  $b$  show a negative correlation between

$\tilde{S}_{st}$  and  $Q_s$  ( $p<0.01$ , Figure 9A), but do not indicate any linear relationship between  $I_\delta$  and  $Q_s$  (Figure 9B). Under even this condition, a negative correlation between  $\tilde{S}_{st}$  and  $Q_s$  and a positive correlation between  $I_\delta$  and  $Q_s$  were approached by a multiple regression analysis, which shows a significant trend for  $Q_s$  to increase as a function of  $-\tilde{S}_{st}$  and  $I_\delta$ :

$$Q_s^* = -0.573\tilde{S}_{st}^* + 0.128 I_\delta^* \quad (r=0.565, F=11.94, p<0.01),$$

where  $Q_s^*$ ,  $\tilde{S}_{st}^*$  and  $I_\delta^*$  are standardized variables of  $Q_s$ ,  $\tilde{S}_{st}$  and  $I_\delta$ , respectively. In this case, a negative relationship between  $\tilde{S}_{st}$  and  $Q_s$  is especially prominent. This relationship, concordant with that of the biometric analyses as shown in Figure 4B, D, strongly supports conspicuous posi-



tive correlation between  $C$  and  $P$  assumed as in the Eq. 6, particularly for simple prisms. As stated above, a positive correlation between  $C$  and  $P$  suggests that both prism size and its variation are mainly controlled either by the growth rate of the entire shell, or by the activity of mantle secretion. If the former is the case, simple prisms must tend to be uniformly large as the entire shell grows faster. On the other hand, if the latter is the case, density of nucleation and growth rate of prisms both must decrease as the secretive activity of the mantle decreases, and a negative relationship is expected between size and the growth rate of simple prisms.

On the other hand, the results of computer simulations with various values of the coefficient  $a$  and the fixed coefficient  $b$  ( $=0.05$ ) show a positive correlation between  $I_s$  and  $Q_s$  ( $p < 0.01$ , Figure 9D), but no significant relationship between  $\bar{S}_s$  and  $Q_s$  (Figure 9C). A multiple regression analysis for  $Q_s$  on  $\bar{S}_s$  and  $I_s$  provides a significant trend to increasing  $Q_s$  as a function of  $\bar{S}_s$  and  $I_s$ :

$$Q_s^* = -0.393\bar{S}_s^* + 0.686 I_s^* \quad (r=0.582, F=9.99, p<0.01).$$

In this equation, a positive relationship between  $I_s$  and  $Q_s$  is more striking than a negative relationship between  $\bar{S}_s$  and  $Q_s$ . This is concordant with the results of the biometric analyses in species with vertical composite prisms shown in Figure 4A, C. This fact supports the assumption that  $P$  has an inverse relationship with  $L$  as defined in Eq. 6, particularly in vertical composite prisms. This assumption implies that the number of nucleations per unit time interval is fixed to a constant value. In the species having a large nucleation zone, in which the value of  $L$  is large, maintenance of the probability of nucleation inevitably causes a large number of nuclei. If we assume an upper limit of the total number of nuclei per unit time interval, the probability of nucleation will vary inversely with the width of the nucleation zone. If the total number of nuclei per unit time interval is fixed, the density of nucleation is expected to decrease as the total shell grows faster. In this case, the median size of prisms is controlled mainly by the growth rate of the entire shell. This fact suggests that, in the case of vertical composite prisms, prism size tends to increase as the entire shell grows faster.

### Discussion and conclusion

Wada (1961) studied the size of crystals in a nacreous shell layer of *Pinctada martensii* in relation to the rate of calcium carbonate deposition. He demonstrated that when the rate of shell deposition is at a maximum, a large number of small crystals occurs on all the nacreous surfaces, while larger crystals occur as the rate of deposition decreases. In addition, Wada (1972, 1985) also reported an inverse relationship between them for such bivalves as *Pinctada fucata*, *Pinna attenuata* and *Hyriopsis schlegelii*. Wada assumed that the primary factor determining size of crystals was the degree of calcium carbonate concentration in the extrapallial fluid. He regarded the rate of calcium carbonate deposition as the rate of crystal growth, and thought that larger crystals tend to grow slowly at a low degree of supersaturation of the fluid, at which the frequency of nucleation diminishes. The results of the present study may

partly support those of Wada, since the negative correlation between size and growth rate of crystals is also expected in this study if the size of prisms is assumed to be controlled by the activity of mantle secretion.

Unlike prismatic structure, nacreous structure does not form the outermost shell layer in bivalves. In the nacreous layer, deposition corresponds to thickening of the shell or growth of crystals, rather than growth of the entire shell. Therefore, the size of crystals in the nacreous layer correlates with the rate of crystal growth rather than with the growth rate of the entire shell. On the contrary, the net growth rate of the entire shell, which reflects the growth rate of the soft parts, seems to be significant for the size of crystals which constitute the outermost shell layer.

Ubukata (1994) claimed that relatively rapid growth of prisms produces prisms prominently inclined to the outer shell surface, because of retardation of the initiation of their forward growth relative to the radial direction. Although such inclined prisms are commonly found in species belonging to Unionidae and Ostreidae (Ubukata, 1994), their prisms also characteristically fell in low (small size) and high  $Q_s$  (irregular in size) regions in Figure 4A, B (refer to Table 1 for higher taxonomy). The present study suggests that such a pattern is produced under the condition of either rapid growth of prisms or slow growth of the entire shell. Ubukata (1994) demonstrated that the relative growth rate of prisms to that of the entire shell determines the orientation of elongation of the prisms.

This study suggests that the sizes of prisms and their size variability correlate with the growth rate of the shell in bivalves. It is well known that internal microgrowth increments often provide a high-resolution record of growth rate and physiological condition of a bivalve (Lutz and Rhoads, 1980), particularly in species with crossed lamellar and horizontal composite prismatic shells. In simple prismatic and vertical composite prismatic shells, however, it is hard to estimate the growth rate of the shell from an analysis of internal microgrowth increments, because periodic growth increments tend to be obscure. The size-frequency distribution of prisms may be a promising index for estimating the growth rate of a fossil bivalve shell.

This study indirectly estimates the relationship between the size of prisms and the growth rate of the shell or prisms from computer simulations, but the direct observation of the growth rate of the shell or prisms remains to be performed. An experimental study on growth of a shell and/or crystals may be required for clarifying the relationship between the crystal size and the growth rate more clearly, and for obtaining a regression equation to predict the growth rate from prism size. The growth rate of the shell and/or crystals is clearly related to the physiological condition of a fossil organism, and has the potential to inspire a research field of 'paleophysiology'.

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## Evolution in morphometric traits in North American Collignoniceratinae (Ammonoidea, Cephalopoda)

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**Abstract.** Eight species and one subspecies of two genera of Collignoniceratinae, *Collignoniceras* and *Prionocyclus*, are analysed with respect to standard morphological distance measures and rib-frequencies, methods of multivariate statistical analysis, including canonical variate ordination, principal components and generalized distances. It was found that the biostratigraphically inferred evolutionary sequence, as currently perceived, is upheld in detail for the *Collignoniceras* data. The 'nearest-neighbour' relationships between the *Prionocyclus* part of the sequence is less complete, although links in main branches are supported. The other aspect given consideration, that of "gracile" and "robust" shells (based on visual inspection of the conch), yielded the result that the subjective assignation of shells to gross morphological type is largely, though not unequivocally, upheld by the statistical analysis. Illustrations of typical representatives of the species analysed are provided.

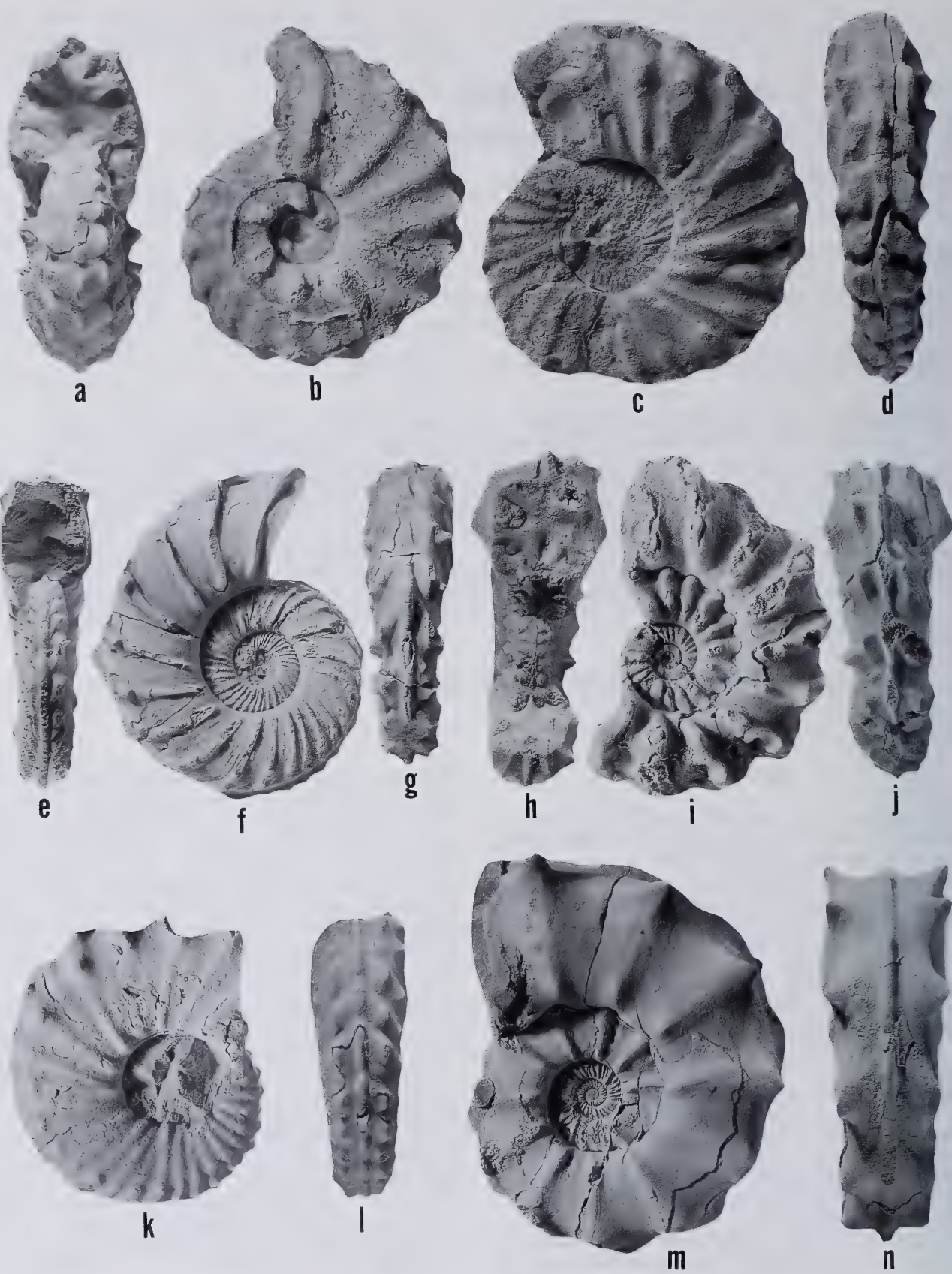
**Key words:** Ammonites, Collignoniceratinae, compositional analysis, Cretaceous of U.S.A., evolution, morphometrics

### Introduction

Ammonite taxonomy is perforce largely based on external morphology—mode of coiling, tuberculation, ribbing and carination. The diagnostic significance of the suture line seems to have been recognized as being of secondary importance for many groups of Jurassic and Cretaceous ammonites (cf. Pérez Claros, 1999). Reyment and Kennedy (1998) and Reyment and Minaka (2000) recorded and described polymorphism in ornamental properties of Cretaceous ammonites of the genus *Neogastrolites*. However, it is by no means a trivial matter to distinguish between true polymorphism, in the classical genetic sense of the property (Falconer, 1981, p. 42; Manly, 1985, p. 402; Roughgarden, 1979, p. 259), and the merging of ornamental types in response to ecophenotypic variation of the kind that seems to occur in the present material with respect to the categories referred to as being 'gracile' and 'robust'. The functional significance of such differentiation, if any, remains obscure. A palaeobiological treatment of the problems involved, and methods for their analysis, are given in Reyment (1991), chapters 5, 6 and 8.

The primary aim of the present study is directed towards ascertaining to what degree the stratigraphically supported

phylogeny within a subfamily of ammonites arrived at by the traditional methods can be recognized by the quantitative analysis of external morphological characteristics (excluding sutures); that is, mainly distance measures on the shape of the shell, but also ribbing density. With such information available, it should become possible to extrapolate to other groups and to work towards stabilizing phylogenetic relationships on less subjective grounds than are yielded by purely descriptive procedures. As far as is known to us, there have been no studies devoted to ascertaining to what extent, if any, wholly distance-related variables are correlated with evolutionary status in ammonites (and, by extension, whether such differentiation can represent a relationship between form and function). The work accounted for in this note shows, with reasonable clarity, that such is indeed the case, at least in the evolution of the Collignoniceratinae. There is, moreover, a more far-reaching consequence to our project. Gross morphology, such as is expressed in coiling and whorl shape, has not been attributed importance of the first order in many evolutionary and taxonomical studies known to us. As we demonstrate in this note, there is information of evolutionary significance in characters of this kind, but it can only be effectively extracted by means of appropriate quantitative procedures in a multidimensional





perspective. The detailed classical taxonomy of the material considered here is scheduled to appear in a separate monograph (Kennedy *et al.*, in press). In order to avoid eventual misunderstanding, we are not concerned with the cladistics/phenetics confrontation; our analysis is solely multivariate morphometric in nature as defined by Blackith and Reyment (1971).

### The material analysed

Members of the subfamily Collignoniceratinae that inhabited the Cretaceous Western Interior seaway of the United States first appeared in the Lower Turonian and ranged into the Upper Turonian. On a mondial scale, the subfamily arose in the uppermost Cenomanian and died out in the Coniacian. The analysis reported here is based on data being presented elsewhere in Kennedy *et al.* (in press), to which monograph reference is made for details of taxonomy, provenance and stratigraphy. Owing to the scarcity of available specimens of some of the species concerned, the phylogenetic study is somewhat less complete than we should have liked it to be. Hence, the conclusions put forward here are necessarily of a preliminary nature.

The earliest Collignoniceratinae of the preserved sequence considered here is the monospecific genus *Cibolaites* Cobban and Hook 1983, of which neither its whence nor its whither seem to be known with any certainty. The genus is distinguished throughout most of its ontogeny by the presence of umbilical, ventrolateral and siphonal tubercles. Its mature body chamber is flat-sided, with progressively weakening tubercles and ribs (Cobban and Hook, 1983, p. 16–18, pl. 2, figs. 1–9; pl. 3, figs 3–8; pl. 8, figs 6–8; pl. 13, figs 1–5; pl. 14, fig. 14).

*Collignonicerases woollgari* (Mantell, 1822) is believed to have descended from *Cibolaites*. It is thought to have given rise to several contemporaneous species in western Europe (Kennedy *et al.*, 1980). In the region under consideration, four successive species seem to have derived from it (presumably via its subspecies *C. w. regulare* Haas, 1946, although the ensuing multivariate study leaves this undecided with respect to the actual route that may have been followed), of which one is considered in the present analysis, to wit, *C. praecox* Haas, 1946; the other three are not available in sufficient numbers for study. *C. praecox* differs from *C. woollgari woollgari* and *C. woollgari regulare* by the persistence of long and short ribs with ventrolateral tubercles out-

numbering the umbilical, and a near-continuous siphonal keel. As shown by the results of the morphoevolutionary analysis, the inferred biostratigraphical relationships between successive species may be a simplification of the actual evolutionary sequence of events.

The later Turonian history of the Collignoniceratinae in the U. S. Western Interior is considered to be marked by the evolution from *Collignonicerases praecox* of species of *Prionocyclus*. Juveniles of species of the two genera can be distinguished in that the keel of *Collignonicerases* has siphonal clavi equal in number to the ventrolateral tubercles, whereas in *Prionocyclus* Meek, 1872, the serrations outnumber the ribs. It is significant that *Prionocyclus hyatti* Stanton, 1894, an early representative of the genus, is morphometrically closely allied to *Collignonicerases woollgari regulare* and somewhat less so with its putative ancestor, *C. praecox*. In general terms, there is semiquantitatively manifested intraspecific variation in the strength of the ornament of most of the species of the Western Interior Collignoniceratinae, a 'gracile' category and a 'robust' one. These are not discrete morphological categories such as are recorded by Reyment (1971) for the genus *Benueites*. Testing the soundness of this interpretation of morphological variability forms an integral part of the analysis presented in the following. Figures 1–3 provide illustrations of typical representatives of the species considered, including examples of shells determined as being robust or gracile.

### Methods

Photographs of the specimens passing muster for statistical study were scanned and the coordinates of seven sites (Figure 4) considered diagnostic were recorded, using the digitization program *TpsDig* written by F. James Rohlf (SUNY at Stony Brook, USA). Only complete specimens were selected for analysis; the numbers of each of the samples of the species are recorded in Table 1. The required distances were computed from these coordinates by simple geometry. This is freely admitted to be an arbitrary manoeuvre and we have desisted from confusing the issue by not calling the coordinate pairs thus obtained "landmarks". In any event, they cannot be equated to the landmarks used by Johnston *et al.* (1991) in their analysis of spiral growth in gastropods. The approach utilized in that study is clearly one that should prove eminently useful in future studies of growth and shape-variation in ammonites, not

← **Figure 1.** a, b. *Cibolaites molenaari* Cobban and Hook, 1983. USNM 498205, a robust form from USGS Mesozoic locality D8429, sec. 1 and NE 1/4 sec. 12, T. 4N., R. 19W., Cibola County, New Mexico. Mancos Shale, from limestone concretions 24–30 m below the top of the Rio Salado Tongue. c, d. *Collignonicerases woollgari woollgari* (Mantell, 1822). USNM 356903, a gracile form from USGS Mesozoic locality D 10243, E 1/2 NE 1/4 sec. 9, T. 5S., R. 2E., Socorro County, New Mexico, Rio Salado Tongue of the Mancos Shale. e–j. *Collignonicerases woollgari regulare* (Haas, 1946). e–g. USNM 498237, a gracile form from USGS Mesozoic locality 21792, west of Newcastle, in the NE 1/4 sec. 31, T. 45N., R. 61W., Weston County, Wyoming, limestone concretions in the Carlile Shale, 18.3 m below the base of the Turner Sandy Member. h–j, USNM 498244, a robust form from USGS Mesozoic locality D9896, NE 1/4 sec. 35, T. 46N., R. 63W., Weston County Wyoming, limestone concretions in the Carlile Shale, 18.3 m below the base of the Turner Sandy Member. k–n. *Collignonicerases praecox* (Haas, 1946). k, l, USNM 498272, a gracile form from USGS Mesozoic locality D 13832, sec. 35, T. 8S., R. 1E., Fall River County, South Dakota, from limestone concretions in the lower part of the Carlile Shale. m, n, USNM 498266, a robust variant from USGS Mesozoic locality D 10697, S E 1/4 SE 1/4 sec. 18, T. 9S., R. 2E., Fall River County, South Dakota, limestone concretions in the Carlile Shale 6 m below the base of the Turner Sandy Member. USGS: United States Geological Survey; USNM: U.S. National Museum of Natural History, Washington D.C. All figures are  $\times 0.9$ .









**Figure 3.** *Prionocyclus wyomingensis* Meek, 1876. Paralectotype, USNM 7729, a gracile form from the Wall Creek Member of the Frontier Formation near Medicine Bow, Carbon County, Wyoming. USNM: National Museum of Natural History, Washington D.C. Natural size.

least because of the finding that mean-forms with similar shapes at the same arbitrary growth increment may have achieved that shape in different ways. The resulting data, suitably corrected for slight differences in magnification from specimen to specimen, were studied by standard multivariate analyses made on the distance measures between adjacent sites and the maximum breadth of the last whorl. The

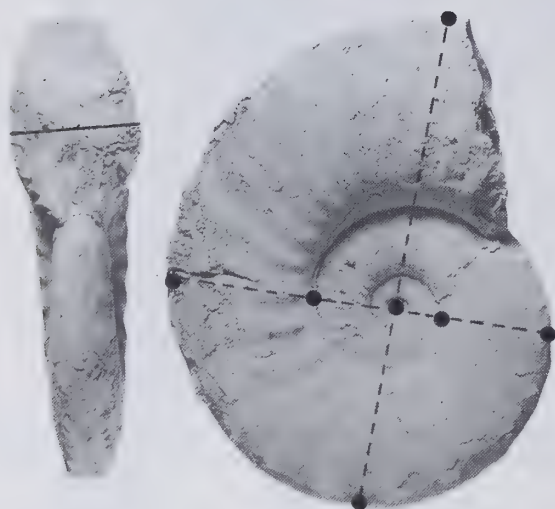
factor of ornamental complexity was introduced into the analysis by appending rib counts to the data matrix. This latter addition accounts adequately for the morphological categories gracile/robust.

The multivariate statistical methods most useful for our study were found to be (1) principal component analysis of the distances (six in all) and the breadth, maximum directly

← **Figure 2.** a–d. *Prionocyclus hyatti* (Stanton, 1894). a, b, USNM 498308, a robust form from USGS Mesozoic locality D3884, Arroyo Lopez, 1 km. north of Holy Ghost Spring, Sandoval County, New Mexico, Mancos Shale, from lower part of Semilla Sandstone Member. c, d, USNM 498323, from USGS Mesozoic locality D 11208, NE 1/4 sec. 36, T. 6N., R. 19W., Cibola County, New Mexico, from the D Cross Member of the Mancos Shale. e–h, *Prionocyclus macombi* Meek, 1876. e, f, USNM 498341, a robust form from USGS Mesozoic locality D4395, north of Rio Gallina in SE 1/4 sec. 15, T. 20N., R. 1E., Rio Arriba County, New Mexico, Mancos Shale, from the base of the Juana Lopez Member. g, h, USNM 498348, a gracile form from the same locality and horizons as c, f. i–m. *Prionocyclus novimexicanus* (Marcou, 1858). i–k, USNM 498434, a gracile form, from USGS Mesozoic locality D9833, NW 1/4, NW 1/4 Sec. 33, T. 40N., R. 82W., Natrona County, Wyoming, from the second ledge forming sandstone below the top of the Frontier Formation. l, m, USNM 498446, a robust form from USGS Mesozoic locality D6928, NE 1/4, SE 1/4 sec. 31, T. 22N., R. 75W., Albany County, Wyoming, from the Wall Creek Sandstone Member of the Frontier Formation. n–q, *Prionocyclus germari* (Reuss, 1845). n, o, USNM 498458, a gracile form from USGS Mesozoic locality D9118, NW 1/4, NE 1/4 sec. 4, T. 33N., R. 81W., Natrona County, Wyoming, from the uppermost sandstone of the Wall Creek Member of the Frontier Formation. p, q, USNM 498483, from the same horizon and locality as n, o. USGS: United States Geological Survey; USNM: National Museum of Natural History, Washington D.C. All figures are  $\times 1$ .

**Table 1.** The biostratigraphical sequence for the species included in the analysis and sample sizes. The asterisks denote species currently used as zonal indices in the Turonian sequence of the Western Interior USA.

Substage	Species	N
UPPER TURONIAN	<i>Prionocyclus germari</i> *	24
	<i>Prionocyclus novimexicanus</i>	10
	<i>Prionocyclus wyomingensis</i>	6
	<i>Prionocyclus macombi</i> *	16
MIDDLE TURONIAN	<i>Prionocyclus hyatti</i> *	19
	<i>Collignonicerias praecox</i> *	12
	<i>Collignonicerias woollgari</i> *	26
LATE LOWER TURONIAN	<i>Cibolaites molenaari</i> *	7



**Figure 4.** Locations of the points observed on the shells superimposed on a gracile specimen of *Prionocyclus macombi* Meek, 1876.

observed diameter and ribbing density, (2) principal coordinate analysis of the coordinate data, and (3) canonical variate analysis of the distance measures in "ordination mode". Unless otherwise stated, the measures were logarithmically transformed. The use of this transformation tends to stabilize the multivariate distribution of the data and to minimize the effects of size differences. Accounts of these procedures applied in like situations are to be found, for example, in Reymont (1991) and Reymont and Savazzi (1999), including examples of the computational procedures applied here and exemplified by ammonite data. Additionally, comparisons between species were made by standard procedures of generalized statistical distance analysis (for the larger samples), backed up by one-way univariate analysis of variance.

The links indicated by the superimposed minimum span-

ning tree on the plots are certainly not infallible statements of fact. For this reason, relationships between species have been further illuminated by means of pair-wise contrasts between latent vectors (principal components) of the logarithmic covariance matrices of the individual samples. Almost all multivariate "variability" in samples is located to the first latent root. For the most part, the smallest latent roots are almost zero and hence the associated latent vector may be considered as representing an almost invariant linear relationship between variables, as was suggested by Gower (1967). A somewhat similar approach to the study of variation in the shape of ammonite shells is outlined in Neige and Dommergues (1995).

## Findings

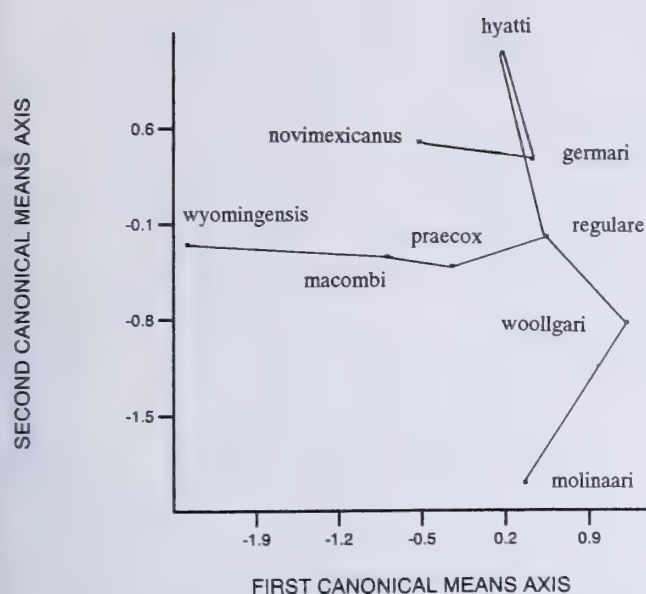
### Ordination of canonical variate means

A useful morphometric tool is often provided by the minimum spanning tree superimposed on the plot of the canonical variate means (Reymont and Savazzi, 1999). This gives the standard ordination of multivariate means a nearest-neighbour categorization. A partial analogy with stars in the firmament serves to illustrate this—stars that to the unaided eye seem to be close to each other can actually lie at extremely great distances from each other in the third dimension. The analyses accounted for in this section are designed to see how well morphometric and morphological characters can reproduce the inferred phylogeny of the lineage.

The first set of means was obtained from the canonical variate extraction in covariance space of the logarithms of the distances between seven sites and nine samples, augmented by directly measured maximum breadth of the shell and ribbing frequency counts in relation to directly measured diameter. How well then is the inferred evolutionary succession based on traditional procedure mirrored in the coiling and ornamental properties of the species of the lineage? In Figure 5, the canonical variate means are seen to divide into two branches. The sequence shown in Figure 5 indicates implied relationships with respect to form within the collignoniceratinid lineage. The minimum spanning tree for the means is superimposed on both plots. It is seen that *C. molenaari* is markedly distant from all other species, as is reflected in its being a monospecific genus established by traditional criteria. This observation accords with the supposition that the morphological passage from *Cibolaites* to *Collignonicerias* was abrupt ('punctuated' as it were). The ordinated linkage order goes from *C. w. woollgari* to *C. w. regulare* to *P. hyatti*, on one branch, and from *C. w. regulare* to *C. praecox* to *P. macombi* Meek, 1876, to *P. wyomingensis* Meek, 1876, on the second branch. However, we shall see in the following that in some relationships, *P. hyatti* tends to behave as though it were a *Collignonicerias*, a peculiarity it does not share with the other representatives of the genus included in our study, and which may reflect its middle-of-the-road evolutionary and morphological status between *Collignonicerias* and *Prionocyclus*.

A minimum spanning tree cannot be expected to provide a mirror image of an inferred phylogenetic sequence. What





**Figure 5.** Minimum spanning tree superimposed on the plot of the first two canonical variate means for 7 distance measures (6 coordinate-based and maximum breadth of the conch), one frequency (ribbing) and 9 groups (the species and subspecies). Analysis made on the covariances of the logarithmically transformed data.

it is designed to seek is morphometric nearness relationships free of any obligatory time constraint. It is therefore interesting to be able to record that the multivariate analytically obtained results reflect rather well the phylogenetic indications based in part on biostratigraphical context. Many of the samples are small and it is encouraging that the results yielded by this analysis are so clearly manifested. In general, it seems clear that the observed stratigraphical ordering of the species is upheld, grosso modo, by the morphometric ordination. We note that, excluding the small samples (to wit, *woollgari woollgari*, *praecox*, *wyomingensis*), all generalized statistical distances between samples are highly significantly different.

In order to test the reliability of results obtained for such small samples, an alternative canonical variate model was used (Reyment and Savazzi, 1999). Here, all values were reduced to standard size by division of them by the maximum diameter of the shell. This standardization has a subsidiary effect, notably, that it transforms the data into compositions, and, consequently, the variables to parts. (N. B. it is fairly common practice in ammonite "biometry" to make scatter plots of ratios and then to look for meaningful constellations of points—statistically, this is not sound procedure.) This change in statistical properties necessitates a methodology appropriate to (constrained or "closed") simplex space (Aitchison, 1986). The multivariate analysis was therefore made on the log-ratio covariances (which involves the loss of one dimension due to the division by one of them). The ordination illustrated in Figure 6 differs in several respects from the foregoing (full-space) version in that

*P. germari* (Reuss, 1845) is quite out of place in relation to the evolutionary succession. The morphoevolutionary passage from *C. molinaari* through the two subspecies of *Co. woollgari* is, however, maintained. We note that *P. hyatti* is now relegated to a branch of its own. Sidestepping the anomalously located *P. germari*, there is a branch that runs from *C. woollgari* s. l. through *C. praecox*, *P. macombi*, *P. wyomingensis* and *P. novimexicanus* (Marcou, 1858), the latter being registered as a branchoff from *P. macombi*. Apart from the anomalous location of *P. germari*, the result illustrated in Figure 6 is in many respects more closely compatible with the conventionally established succession of species than Figure 5. The main point to be heeded is, however, that the linkages are essentially the same in both representations, notably the *Cibolaites*–*Collignonicerates* sequence and the *C. praecox*–*P. macombi*–*P. wyomingensis* passage.

#### Results obtained by the principal component analysis of the distances

For the purposes of this part of the analysis, two latent vectors turned out to be of special interest. The latent root attached to the first latent vector is overwhelmingly large in relation to the other roots. The smallest latent root is virtually zero and hence may be considered to be an expression of an almost invariant linear relationship between the variables (Gower, 1967). Such an invariant relationship is of special taxonomic and hence phylogenetic interest because it represents a linear combination that is intrinsically bound to the form under consideration. The species studied in this connexion are: *C. woollgari woollgari* and subspecies *C. w. regulare*, *C. praecox*, *P. hyatti*, *P. novimexicanus*, *P. macombi* and *P. germari*. We wish to make it clear that the method of comparison of angles (Blackith and Reyment, 1971) is not a statistical technique, being rather a procedure appropriate to *ad hoc* data-analysis. Nonetheless, it has proven itself to be useful in many taxonomic studies.

#### The first principal component

This section is concerned with examining how morphometrically divergent succeeding species in the evolutionary succession are from each other. The angles between pairs of first latent vectors and sixth latent vectors, respectively, are listed in Table 2. The angles for the first latent vector for the comparisons of *C. molinaari* and *C. w. woollgari*, respectively *C. w. regulare* are almost identical (21.33°, respectively, 21.88°). This interesting result indicates not only that the ancestral species is separated by a strongly expressed morphological jump from its descendants, but also that the angle between ancestor and descendant subspecies is identical and that the two subspecies of *C. woollgari* are morphologically close to each other. This observation is supported by the small angle between these two subspecies, namely, 2.21°. The species next in the stratigraphical hierarchy is *C. praecox*, the angle between its first latent vector and both subspecies of *C. woollgari* being the same, to wit, 9.56°. The angle between *C. praecox* and *P. hyatti* is quite small, being 4.82°, whereas that between *P. hyatti* and *P. macombi* is 6.24°. The next passage from *P. macombi* to *P. wyomingensis* is connected with a small an-



**Table 2.** Angles between first and sixth latent vectors (covariance matrix of logarithmically transformed variables) for critical pairings. The asterisk denotes comparisons made on very small sample sizes. Co=*Collignonicer*as, Ci=*Cibolaites*, P.=*Prionocycl*us.

Comparison between	Angle for vector I	Angle for vector VI
<i>Ci. molenaari</i> / <i>Co. woollgari woollgari</i> *	21.33	87.80
<i>Ci. molenaari</i> / <i>Co. woollgari regulare</i> *	22.88	38.75
<i>Co. woollgari woollgari</i> / <i>Co. praecox</i> *	9.56	81.53
<i>Co. woollgari woollgari</i> / <i>Co. regulare</i>	2.21	67.31
<i>Co. woollgari regulare</i> / <i>Co. praecox</i>	9.56	59.54
<i>Co. woollgari regulare</i> / <i>P. hyatti</i>	6.71	20.53
<i>Co. w. regulare</i> / <i>P. germari</i>	3.29	48.23
<i>P. hyatti</i> / <i>P. germari</i>	3.58	33.92
<i>Co. praecox</i> / <i>P. hyatti</i>	4.82	90.00
<i>Co. praecox</i> / <i>P. macombi</i>	5.45	54.06
<i>P. macombi</i> / <i>P. wyomingensis</i> *	3.18	88.10
<i>P. novimexicanus</i> / <i>P. germari</i>	7.73	46.06

gular difference, notably, 3.18°. There is a notable leap in the angle between the first latent vector of *P. wyomingensis* and its descendant *P. novimexicanus*, namely 11.24°. The final link, from *P. novimexicanus* to *P. germari* is accompanied by an angular divergence of 7.73°. It is significant that the angular divergences between latent vectors of the *Prionocycl*us sequence are mostly of the same order of magnitude.

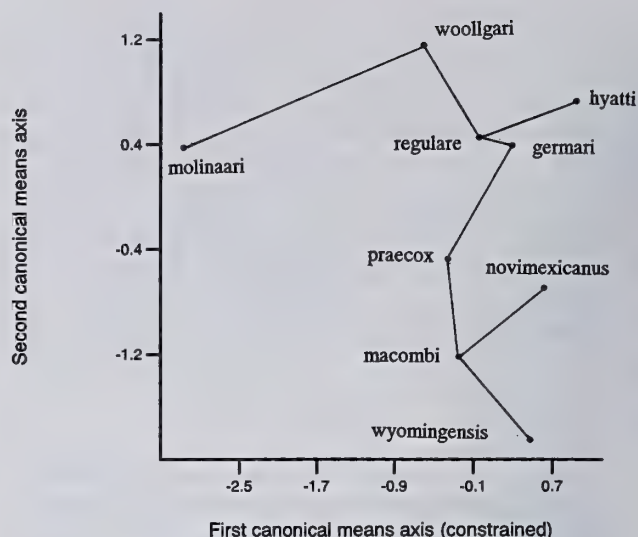
Comparisons made for the 'smallest' latent vectors are all noticeably greater. This could conceivably indicate that intrinsic morphometric specific differences are to be found in the (almost) invariant principal component, granted that the first latent vectors, which are all connected to more than 98% of the total variability, are so similar. The more interesting of these relationships are:

1. *Cibolaites molenaari*-*Collignonicer*as *woollgari* subspecies. The angles for vector I are here almost identical, as reported above. The values for vector VI differ strongly, with the angle between the vectors for *molenaari*-*C. woollgari woollgari* being almost a right angle, whereas that for the comparison with *regulare* is a relatively low 38.75°.

2. *Collignonicer*as *praecox*-*C. woollgari* subspecies. The angular differences for vector VI are large, being essentially greater for the comparison with *C. woollgari woollgari*. The angular differences for the comparisons between first latent vectors are small, and smallest for the latter subspecies.

3. *C. praecox*-*P. hyatti*. The result yielded here is noteworthy. The first latent vectors are almost collinear, which hardly accords with the linkage in Figure 6 yielded by the minimum spanning tree. However, the value for vector VI places these vectors exactly at right angles to each other. We are inclined to accept this result as indicating support for the view that the invariant latent vector of distances harbours taxonomically relevant information.

4. The plot in Figure 6 shows *C. w. regulare* and *P. germari* to be located near to each other, but the linkage sequence does not indicate these two taxa to be close. Comparison of the smallest latent vectors yields a relatively



**Figure 6.** Minimum spanning tree superimposed on the plot of the first two canonical variate means for the same set of data as in Figure 5, but standardized with respect to size (hence in compositional mode). Analysis made on the log-ratio covariances (cf. Aitchison, 1986).

large angle, namely 48.23°.

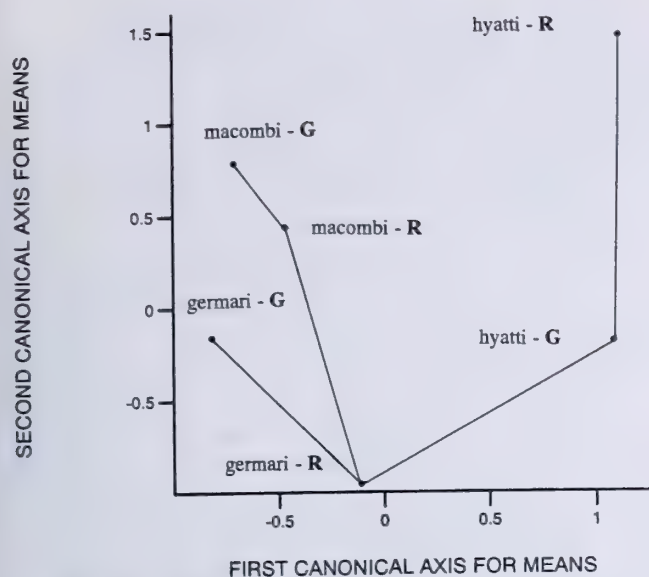
5. *C. w. regulare*-*P. hyatti*. The biostratigraphical scheme leads one to expect that *C. praecox* would be more like *P. hyatti* than *C. w. regulare*, considering that it has been put forward as the logical ancestor of the former, and this is indeed implied by the angle between the first latent vectors, being among the smallest of the entire set of values reported in Table 2 and, in effect, denoting collinearity. However, the angle between vector VI for these two taxa is by far the smallest of all and it seems that it is this relationship that is reflected in the pattern obtained for the minimum spanning tree (Figure 5).

6. Anomalous large angular differences occur for the pairings *macombi*-*wyomingensis* and *wyomingensis*-*novimexicanus*, probably due to the small sample sizes involved. We note that the sample size for *P. wyomingensis* is beneath the level for a resolvable covariance matrix (i.e. more variables than specimens).

### Robust vs gracile shells

The routine taxonomic appraisal of the material (Kennedy, 1988) suggested that there are two classes of ornamental categories in the species of the genera considered here, to wit, robustly ornamented shells and finely ornamented shells (the gracile shell-type). These do not appear to be morphs of the kind described by Reymont and Kennedy (1998). Only three species occur in sufficient numbers to permit statistical appraisal of these categories- *P. hyatti*, *P. macombi* and *P. germari*. The same suite of methods as were used for the full set of observations were applied to the reduced set, noting that there are now 6 groups for 6 distance measures. In Figure 7, the canonical variate means for the two ornamental categories for these three species are plot-





**Figure 7.** Minimum spanning tree superimposed on the canonical variate means for robust and gracile categories of three species of *Prionocyclus*, based on 6 distance measures and 6 groups (three "robust" classifications and 3 "fragile" classifications).

**Table 3.** Angles between first and sixth latent vectors for the robust/gracile data for critical pairings of three species of *Prionocyclus*

Comparison between	Angle for vector I	Angle for vector VI
<i>germari</i> G/ <i>germari</i> R	1.99	41.07
<i>macombi</i> G/ <i>germari</i> R	1.87	85.40
<i>germari</i> G/ <i>hyatti</i> G	2.21	55.62
<i>germari</i> G/ <i>macombi</i> G	3.35	7.91
<i>hyatti</i> G/ <i>macombi</i> G	5.22	56.69

ted and linked by the superimposed minimum spanning tree. The most notable feature of the plot is that robust and gracile shell-types for each species, respectively, are linked, and that their means do not coincide, or almost coincide in location. Hence, differences in multivariate means of the subjectively identified categories are tangible, but not so great as to confuse taxonomic issues. In Figure 7, we show the plot of the individual points in the plane of the first two canonical variate axes (i.e. the canonical variate scores on the first two axes). The points for the six categories group naturally with gracile and robust forms for each species being nearest neighbours. Links between species are the union of robust *germari* to robust *macombi* and robust *germari* to gracile *hyatti*.

Comparisons of the first and sixth principal components lead to interesting consequences (Table 3). All angles between various comparisons of first latent vectors of the logarithmic covariance matrix are low. Note particularly the values for *germari* and *macombi*, 1.99° and 1.87° respec-

tively. The angles for the sixth latent vectors are large and generally of the same order of magnitude as found for the complete data-set, but with one striking exception, notably, the comparison between gracile individuals of *germari* and *macombi*, 7.91°. This would seem to point to a close morphometrical relationship between the two species, which is possibly of taxonomical significance.

Doubtlessly, the gracile/robust subsamples yield a more structured multivariate statistical analysis than do the full samples. Granted that the taxonomic integrity of the subsamples was not infringed upon by the partitioning, it may be suggested that the qualitatively arrived at subdivision into two morphological types is largely justifiable.

The question now arises as to how morphometrically similar are the two categories *robust* and *gracile*? The material is not sufficiently comprehensive to allow categorical assertions. However, the data for *P. germari* may be taken to serve as a guideline. Robust *germari* links to robust *macombi*, thus implying a certain degree of ornamental homogeneity, whereas robust *germari* links to gracile *hyatti*. Figure 7 intimates also that *germari* and *macombi* are morphometrically more alike than either is with *hyatti*. This observation adds further evidence with respect to the transitional evolutionary status of *Prionocyclus hyatti*, which in many features displays morphometrical properties of *Collignonicer* type.

## Conclusions

The multivariate-morphometrical analysis of a sequence of Collignoniceratinae from the Turonian of the U. S. Western Interior has brought to light several features of general interest for the study of evolution in ammonite morphometry with respect to the property of coiling. This result is somewhat unexpected, granted that coiling in shell-bearing cephalopods is under the rigid constraint imposed by the biomechanism determining logarithmic growth. These are:

1. The species of *Collignonicer* align in accordance with biostratigraphical observations, thus preserving generic integrity and evolutionary status. The passage from *Cibolaites* to *Collignonicer* is abrupt, a saltation as it were.
2. The passage to *Prionocyclus* is slightly less well manifested in that there is a dichotomy in the relationship implied by the minimum spanning tree with *P. hyatti* occupying, jointly with respect to linkage (but naturally not time), an evolutionary position on a par with *C. praecox*. In this respect, the former species behaves in some cases as though it were a *Collignonicer*. The dichotomous impression is further strengthened by the passage of *praecox* to *macombi* which in turn, links to *wyomingensis* (in agreement with the biostratigraphical inference—cf. Table 1).
3. The second branch in Figure 5 lets *hyatti* link directly to *germari* and *novimexicanus*. In Figure 6, *hyatti* is located on a separate branch. This result accords with the transitional status of this species, as indicated by the results of the present study.
4. The qualitative observations leading to the recognition of robust and gracile shell forms in all species can be upheld in part, as far as can be judged from those samples compris-

ing sufficient material for statistical calculations. Also here, the ambiguous evolutionary status of *P. hyatti* is manifested. The possible functional significance of the two shell types would seem to be worth detailed study, possibly in relation to foraging aspects (Reymont, 1988).

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## A review of symbiosis in the Bivalvia, with special attention to macrosymbiosis

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**Abstract.** The symbiosis (defined as a strict interspecific association) between bivalves and other organisms is examined. Microsymbiosis (i.e., symbiosis with microorganisms) is frequent among Recent bivalves, and has been proposed to explain the unusual characters of several fossil bivalves. However, a critical review of the morphological criteria used to infer microsymbiosis in fossil bivalves shows that their application is likely to result in a large number of false positive and false negative results. Symbiosis with macroscopic organisms (i.e., macrosymbiosis), on the other hand, has a better chance of being recognised correctly in fossils, although direct preservation of the associated organisms remains the only completely safe criterion. Recent and fossil instances of macrosymbiosis are reviewed, and new evidence is presented to clarify the adaptive significance of some of these associations.

**Key words:** Bivalvia, chemosymbiosis, commensalisms, functional morphology, Lingulidae, Mollusca, parasitism, photosymbiosis, Porifera, Scleractinia, symbiosis

### Introduction

Symbiosis was originally defined as a strict, usually obligatory association of individuals belonging to two or more species (Bary, 1879). This definition does not imply that the association is mutually advantageous to the organisms involved. Only subsequently was the term used with the latter meaning. The present paper follows the original definition of symbiosis, since no other concise term is available to characterise an interspecific association without connotations of usefulness to the involved organisms. Use of the terms commensalism and parasitism, for instance, requires that the life habits and the advantages and/or disadvantages to the species involved are known.

For the purposes of this paper, two categories of symbiosis can be recognised among bivalves. The first involves microscopic endosymbionts living in a bivalve host. This category can be characterised as microsymbiosis. The second category involves macroscopic organisms associated with bivalves, and can be called macrosymbiosis. This paper concentrates on the latter category, but a discussion of microsymbiosis is useful as an introduction, because this subject has received considerable attention by palaeobiologists (see references below). In addition, this theme illustrates several of the problems that characterise the recognition of macrosymbiosis in the fossil record.

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author.

### Microsymbiosis

#### Photosymbiosis

Most of the literature on symbiosis in bivalves deals with microscopic endosymbionts hosted by bivalves. In particular, photosymbiotic zooxanthellae and the associated adaptations of the hosts have been studied in the Recent Tridacnidae (Yonge, 1936; Purchon, 1955; Stasek, 1961, and references therein) and Cardiidae (Kawaguti, 1950, 1968, 1983; Hartman and Pratt, 1976; Jacobs and Jones, 1989; Jones and Jacobs, 1992). The host bivalves show a range of cytological adaptations to the symbionts, as well as microstructural and macroscopic adaptations in shell morphology (e.g., see above references, and Seilacher, 1972, 1973, 1990).

Among these bivalves, the Tridacnidae build extremely large and thick shells thanks to photosymbiosis, and their ventral commissure (uppermost in the life position) is modified to maximise exposure of the mantle tissues to sunlight. In some species, sculpture on the external shell surface further increases the mantle area exposed to light (above references).

The cardiid *Corculum* has an antero-posteriorly flattened, semitransparent shell to optimise the exposure of the mantle to sunlight passing through the shell. The posterior shell slope possesses numerous semitransparent windows, which



result from a peculiar type of shell pigmentation rather than from a specialised microstructure (Watson and Signor, 1986).

Other Recent bivalves are known to possess photosynthetic endosymbionts. Among them are the freshwater unionid *Anodonta* (Goetsch and Scheuring, 1926) and the trapeziid *Fluviolanatus sub torta* (Morton, 1982). The significance of these associations has not been studied in detail. Other bivalves are frequently infected by microscopic algae (e.g., the Recent pectinid *Placopecten magellanicus*; Naidu and South, 1970; Naidu, 1971). Although these can be characterised as instances of parasitism by the alga, they are interesting in that they constitute a possible evolutionary stepping-stone toward a mutually advantageous situation.

The adaptive significance of photosymbiosis is not uniform among bivalves. In the Tridacnidae, photosymbionts are an important food-source for the host, and they allow the construction of very large and heavy shells (above references). In all other studied instances, however, the bivalves are relatively small, and their shells thin or only moderately thick. In at least part of these cases, the spectrum of sunlight appears to be selectively filtered by the mantle tissues of the host in order to fine-tune the metabolic products of the photosymbionts (above references).

A few palaeontologists (e.g., Kriz, 1979; Yancey, 1982; Yancey and Boyd, 1983; Seilacher, 1990) have proposed photosymbiosis in a broad range of fossil bivalves, using morphological convergence with *Tridacna* and/or *Corculum* to support their theses. These fossil bivalves range in age from the Palaeozoic to the Caenozoic, belong to several superfamilies, and possess extremely large and/or thick shells, or antero-posteriorly flattened and presumably translucent *Corculum*-like shells.

The reliability of these morphologic criteria to infer photosymbiosis in fossil bivalves, however, is questionable. With the exception of *Corculum* and the Tridacnidae, Recent photosymbiotic bivalves show little or no morphological specialisation of the shell to photosymbiosis. In addition, while photosymbiosis in *Tridacna* is directly related to increased shell secretion and affects its stable-isotope composition (above references), such phenomena are absent in other Recent photosymbiotic bivalves (Jones and Jacobs, 1992). Nonetheless, stable-isotope analysis can be used in fossils when one desires to test whether shell secretion was aided by photosymbiosis, in a manner convergent to the Tridacnidae. Such an analysis led Jones, Williams and Spero (1988) to exclude photosymbiosis (or at least its involvement in shell secretion) in the Pliocene *Mercenaria "tridacnoides"*. This bivalve is a morph of *M. campechiensis*, and differs from the latter in a shell with a wavy or zigzag ventral commissure. Seilacher (1990) had earlier proposed photosymbiosis in this form, based on shell morphology.

Finally, one may test the reliability of the above morphologic criteria by applying them to Recent bivalves. There are several living bivalves which have at least one of the morphologic characters mentioned above. Among these are large and thick-shelled Ostreidae, Spondylidae, Pectinidae and Arcidae. However, none of these bivalves are known to host photosymbionts.

A flattened and translucent shell in an epifaunal bivalve is

not a reliable indication of photosymbiosis, either. A very good example is the Recent anomiid (or placunid) *Placuna placenta*. This species possesses a laterally flattened, thin and very translucent shell (Yonge, 1977, regarded this species as the most flattened bivalve), and is a recliner on the surface of soft sediments in shallow water. Incidentally, the shell of this species was commonly used by the human population of the Philippines for the construction of house windows, before glass became broadly available. In a fossil species, such a shell might be regarded as an indication of photosymbiosis. However, *P. placenta* apparently hosts no photosymbionts. Although I am not aware of any explicit statement to this effect in the literature, the soft tissues were studied extensively by Yonge (1977), who most likely would not have failed to observe photosymbionts if they had been present.

Other Recent species of *Placuna*, like *P. ephippium*, are even larger than *P. placenta*. In *P. ephippium*, however, a reddish or brown pigmentation of the internal shell layer reduces shell translucency, and could be adaptive in sheltering the soft tissues from sunlight. Presumably, this pigmentation would be lost in fossilised material, leading an observer to conclude incorrectly that the shell was translucent like the one of *P. placenta*.

A further example is the Recent endolithic pectinid *Pedum*, which exposes a broad surface of ventral mantle tissues to the ambient light, in a fashion not unlike the Tridacnidae. The mantle tissues of *Pedum* are heavily pigmented and resemble the brightly-coloured ones of the Tridacnidae. However, this species hosts no photosymbionts (Savazzi, 1998). The broad expanse of exposed mantle tissues in *Pedum* does not appear to be adaptive by itself, and is rather a consequence of the mode of growth of this bivalve (see also below).

The presence of a prismatic or fibrous shell microstructure in some large fossil bivalves has been advocated in support of the photosymbiosis hypothesis, on the grounds that such a structure could conduct light well, working like a bundle of optical fibres (e.g., Seilacher, 1990). However, this type of light transmission has not been verified in Recent shell material. In particular, it is not known whether the sides of the prisms (which in living bivalves are interfaces between calcite and organic matrix) act as reflectors, or whether the refraction index at the periphery of the fibres is different from the one at its centre. Either condition is indispensable for the fibre to function as a light guide. The fibrous layers of some fossil bivalves do seem to act as optical fibres, but this could be misleading, since the organic shell matrix in this material was likely lost or altered during diagenesis, so that the prism sides are now calcite/air interfaces with optical properties different from the original ones. In addition, the optical properties of fibrous layers could be irrelevant, because sunlight may have been absorbed by additional shell layers with different microstructures (which, in addition, may have disappeared through selective diagenetic solution), or by a pigmented periostracum or organic shell matrix (see also above).

In conclusion, when performing this type of functional reconstruction, it should be remembered that morphologic criteria alone are unreliable, since flattened and/or thickened



shells may have several adaptive explanations. Therefore, many instances of photosymbiosis inferred from large and thick shells, translucent shells and/or flattened shell geometries in fossils are likely false positives, while most of the true instances of photosymbiosis in fossils are likely to pass undetected.

A few fossil bivalves with highly specialised morphologic features may have been photosymbiotic. This is the case, for instance, of some rudists (Vogel, 1975; Seilacher, 1998, and references therein). Shell morphology indicates that, in several representatives of this group, a well-developed system of mantle diverticula occupied cavities within the shell, and in some cases was also exposed to the outer environment. However, it must be stressed that, based on palaeoenvironmental reconstructions, as well as on the lack of the above morphological features in most rudists, photosymbiosis must have been restricted to few representatives (see Jablonski, 1996).

Another candidate for symbiosis is represented by the Triassic wallowaconchids (Yancey and Stanley, 1999), in which the wing-like lateral carinae of the large *Corculum*-shaped shells were subdivided into partitions by radially-growing septa and, presumably, occupied at least in part by finger-like extensions of mantle tissues. This morphology is compatible with photosymbiosis (assuming the shell was translucent) as well as chemosymbiosis (assuming that the shell cavities housed chemosymbionts). However, septation of the carinae may be functional as a lightweight mechanical reinforcement, and a critical analysis of the symbiosis hypothesis shows that no septa, or at most a single septum separating the space within the carina from the rest of the shell cavity, are required for both photosymbiosis and chemosymbiosis to take place.

In these and comparable instances, photosymbiosis should be regarded as a reasonable hypothesis only if (1) the observed morphology satisfies all requirements for photosymbiosis, and (2) alternative functions for the observed morphology can be discarded. In the rudists with exposed mantle tissues, for instance, one should try first to eliminate the possibility that the mantle functioned as a ciliated carpet for the collection of food particles. In the case of rudists with shell diverticula, one should exclude alternative functions like brood pouches, cavities for the "farming" of chemosymbionts, structures for discouraging attacks by shell borers, energy-absorbing "bumpers" that would stop impact cracks from propagating to the inner shell layers, and lightweight shell structures like those observed in Recent soft-bottom oysters (e.g., cf. Chinzei, 1995). If these precautions are taken, unusual morphological adaptations like those of the rudists and wallowaconchids may be more reliable in inferring instances of photosymbiosis than general criteria based on large massive shells or antero-posterior shell flattening.

### Chemosymbiosis

Chemosymbiosis appears to be more common than photosymbiosis among Recent bivalves. In addition to deep-water forms, like *Calyptogena*, which are associated with hydrothermal vents (e.g., Hashimoto *et al.*, 1989; Horikoshi, 1989) or hydrocarbon seeps (Childress *et al.*,

1986), several deep-infaunal bivalves from shallower water rely on bacterial chemosymbionts. These forms rely on bacteria that oxidise sulphide or methane (above references). In several cases (e.g., the Lucinidae, *Solemya*), the chemicals necessary to feed the symbionts are drawn to the mantle cavity by pumping pore water from deeper, anoxic layers of sediments (Felbeck *et al.*, 1983; Dando *et al.*, 1985, 1986; Reid and Brand, 1986). At least in some of these bivalves, elemental sulphur can be stored within the organism, possibly as a means to store energy (Vetter, 1985).

*Solemya* and *Lucinidae*.—*Solemya* builds Y-shaped burrows, and collects water from underlying, oxygen-poor and nutrient-rich sediment through the lowermost branch of its burrow (Stanley, 1970, pl. 3; Seilacher, 1990). Lucinids use the highly extensible foot to build a system of narrow canals with a comparable function (e.g., see Stanley, 1970, pls. 15–18).

Fossil burrows of *Solemya* (or bivalves with similar habits) have been described as ichnotaxa (Seilacher, 1990), and the burrows of lucinids are potentially preservable. These ichnostructures can be used to detect indirectly chemosymbiosis in these and similar bivalves. However, one must keep in mind that several burrowing bivalves build a single siphonal gallery directed downwards (e.g., see Stanley, 1970). This gallery leads the exhalant current deep into the sediment, and therefore cannot be related to chemosymbiosis.

*Teredinidae*.—Most Teredinidae are wood-borers and host symbiotic cellulose-digesting microorganisms in an enlarged gut (Turner, 1966, and references therein). Thus, these bivalves utilise the substrate as a food source. Chemosymbiosis is not directly reflected in morphological adaptations of the skeletal parts. However, the boreholes of the Teredinidae are uniquely long (up to 2 m) and slender (typically 5–20 mm in diameter), and can "snake" around obstacles and other boreholes, thus allowing these bivalves to utilise the substrate with a higher efficiency than any other wood-borers.

The Caenozoic to Recent teredinid *Kuphus* reaches very large sizes (over 1 m in length, with a diameter of up to 60 mm) and builds a thick calcareous tube. However, this form is not a wood borer but a secondary infaunal soft-bottom dweller (Savazzi, 1982a, 1999b). It is not known whether it utilises the substrate as a food source, and therefore its body volume, which is substantially larger than that of any wood-boring teredinid, remains unexplained.

*Fresh-water bivalves*.—The unionid *Pleiodon adami* from the African Pleistocene possesses a tube-like structure projecting from the antero-dorsal shell margin and parallel to the elongated hinge line. Seilacher (1990) suggested that this tube functioned like a pipette, in order to funnel pore water from underlying sediment layers into the mantle cavity. This would have avoided direct contact of the soft parts with the anoxic sediment. However, Savazzi and Yao (1992) found that other Recent and Pleistocene fresh-water bivalves of similar overall shell morphology (albeit possessing smaller or no anterior projections) burrow with the commissure plane conspicuously inclined, rather than subvertical as inferred by Seilacher for *P. adami*. In the latter species, a subvertical



orientation would seem to be optimal for siphoning pore water from deep within sediment, while a substantially inclined orientation like the one observed in other fresh-water bivalves would place the antero-dorsal pipe in an unfavourable position. Thus, chemosymbiosis would have required *Pleiodon* to assume a shell orientation unusual for these bivalves. Specimens recorded in the life position could help to shed light on this species.

### Conclusions

In spite of numerous attempts, the feasibility of detecting reliably photo- and chemosymbiosis in fossil bivalves appears questionable. All the criteria discussed above for inferring photosymbiosis in fossil bivalves are likely to produce a large number of false positive and/or false negative results. Probably, the fossilised burrows of a few chemosymbiotic bivalves are so far the only reliable evidence of such life habits. However, it cannot be excluded that careful analyses and new evidence may reveal probable instances of photo- and chemosymbiosis among fossil bivalves.

### Macrosymbiosis

Macrosymbiosis in bivalves has received a lesser attention than microsymbiosis, and it is legitimate to ask whether it has a potential for being recognised in fossil material. Macrosymbiosis can be subdivided into two broad categories. The bivalve may be embedded in a larger organism or attached to its outer surface, or the reverse situation may occur.

#### Embedded macrosymbiotic bivalves

*Lithophaginae*.—Several Recent species of the mytilid *Lithophaga* occur constantly within living scleractinian corals (e.g., Kleemann, 1980). This type of association dates at least from the Palaeogene (Krumm and Jones, 1993). Although each of these *Lithophaga* species is recorded from several species of host coral, they are never found in dead corals (which are inhabited by other species of *Lithophaga*, exclusively living in this habitat). The siphonal opening of the borehole is exposed to the external environment, and there is no indication that the bivalve exploits the host as a source of food. Most likely, the living substrate provides better protection (living corals grow, while dead ones are subjected to erosion and/or fouling by encrusters) and possibly a lesser degree of competition by other borers (living corals may be less subjected to bioerosion than dead ones, and the endolithic fauna of living corals is, at any rate, less diverse than that of dead substrates).

Boring in living scleractinians requires the veliger to settle on the epithelium of the host and to pierce it to reach the skeleton. Alternatively, the veliger could be ingested by a coral polyp and subsequently pierce its coelenteron lining. In either case, this appears to require a behavioural and/or biochemical specialisation. It is not known whether *Lithophaga* boring in live coral constitutes a monophyletic or polyphyletic group. These species, at any rate, cannot be distinguished reliably from dead-substrate species on the basis of shell morphology. Several (possibly a majority) of

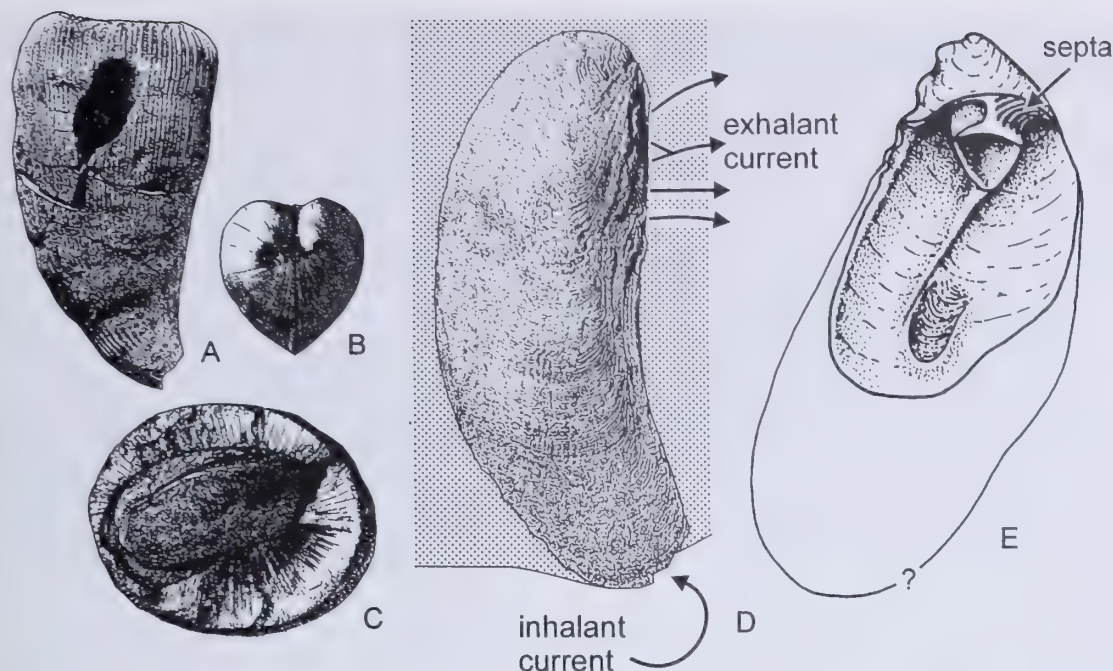
live-coral *Lithophaga* possess a secondary calcareous coating on the outer shell surface. In several cases, this coating forms into structures (aristae, or sets of denticles) that protect the posterior shell commissure against predators (e.g., Savazzi, 1999b, and references therein). Most species of *Lithophaga* that bore in dead substrates are devoid of shell encrustations, but some dead-substrate species possess coatings fully comparable to those of live-coral borers (pers. obs.).

The boreholes of live-coral *Lithophaga* show distinctive morphological characters. The coral surface immediately surrounding the borehole opening is often depressed into a shallow funnel. This feature is absent in dead-substrate *Lithophaga*. In addition, growth of the coral forces the bivalve to move backwards through the substrate, in order to remain close to the external environment. This, in turn, is required by the relatively inefficient filibranch gills of these bivalves (Carter, 1978). The backwards-boring process causes the bivalve to vacate the anterior region of the borehole. This results in a long anterior extension of the borehole, partly filled with meniscus-shaped calcareous septa and/or loose calcareous deposits (Figure 5H). In Quaternary deposits along the coast of Hilotongan Island, the Philippines, the writer observed weathered sections of large coral boulders containing *Lithophaga* backward-boring tracks reaching approximately 1 m in length. Assuming a rate of backward-boring equal to or higher than that of forward-boring (because of the presence of the siphonal opening, backward-boring necessitates the removal of a smaller volume of substrate per unit of length than forward-boring), the observed length of boring tracks is consistent with observations on the Recent rock-boring species *L. lithophaga* by Kleemann (1973, and references therein), who reported a boring rate in limestone of up to 12.9 mm per year and a life span of up to about 80 years.

*Lithophaga lessepsiana* is a small Recent species that bores either in living reef corals or in solitary free-living scleractinians of the genus *Heteropsammia* (Arnaud and Thomassin, 1976; Kleemann, 1980). *Heteropsammia*, in turn, is symbiotic with a sipunculid housed in a spirally coiled cavity in the basis of the coral. *L. lessepsiana* bores within the basis of *Heteropsammia*, and grows to a shell length comparable to the coral diameter, probably causing the eventual death of the coral (Arnaud and Thomassin, 1976). When boring in *Heteropsammia*, *L. lessepsiana* lies with the ventral commissure uppermost (Arnaud and Thomassin, 1976). This species is entirely or almost entirely devoid of secondary calcareous deposits of the external shell surface.

The Recent mytilid *Fungiacava* went one step further and evolved into an endoparasite of fungiid corals (Goreau *et al.*, 1976, and references therein). The siphonal opening of this small form communicates with the coelenteron of the host, from which the bivalve draws its food. *Fungiacava* follows the growth of the host by migrating within its borehole to remain near the coelenteron. Like *L. lessepsiana*, it lies with the ventral commissure uppermost. This habit is recognisable in fossils, because of the placement of the siphonal opening of the borehole in a region of the coral skeleton covered by a considerable thickness of soft tissues. In fact, boreholes of *Fungiacava* were described in





**Figure 1.** A–C. *Botula hortensis* (Lamarck) symbiotic in *Pattalophyllia* sp., Upper Eocene, Possagno, Italy, (Geologisch-Paläontologisches Institut, Tübingen, Germany, GPIT 1571/2–4). Host coral with siphonal opening of borehole (A), anterior view of shell (B) and shell in place within the borehole (C). Shell length is 19 mm. D. Schematic drawing of *Vulsella vulsella* (Linnaeus) embedded in host sponge, Recent, Cebu Island, the Philippines. The surface of the sponge is at the bottom. Shell length is 4 mm. E. *Stefaniniella colosii* Tavani, Cretaceous, Somalia (modified from Tavani, 1941). Height of the preserved shell portion is 85 mm. The extent of the original shell outline (indicated with a question mark) is reconstructed by analogy with Recent *Vulsella* and other malleids.

Pleistocene fungiids (Goreau *et al.*, 1976).

**Botula.**—The Eocene mytilid *Botula hortensis* (Figure 1A–C) was a borer obligatorily associated with living solitary corals (Savazzi, 1982b). Unlike other boring bivalves (cf. Savazzi, 1999b, and therein), *B. hortensis* did not secrete a lining onto the walls of the borehole. Instead, the coral host reacted to the presence of the borer by sealing the spaces between adjacent septa with a secondary calcareous secretion in the region surrounding the borehole. This reaction by the host enables one to detect that the coral was alive at the time it was bored. The borehole of *B. hortensis* opens on the side of the coral theca (Figure 1A).

The corals inhabited by *B. hortensis* were soft-bottom forms attached to a substrate only in their juvenile phase and probably capable of active righting. Their theca is horn-shaped, rather than flattened like fungiids. *B. hortensis* had a life orientation with the ventral commissure uppermost (like *Lithophaga* in soft-bottom corals; see above).

Although morphologically similar to other species of *Botula*, *B. hortensis* differs in behaviour and autecology. Recent *Botula* are mechanical borers in soft rocks and packed mud, while *B. hortensis* appears to be a chemical borer, because its shell is thin, has no specialised sculpture, and yet displays no surface wear (Savazzi, 1982b, 1999b).

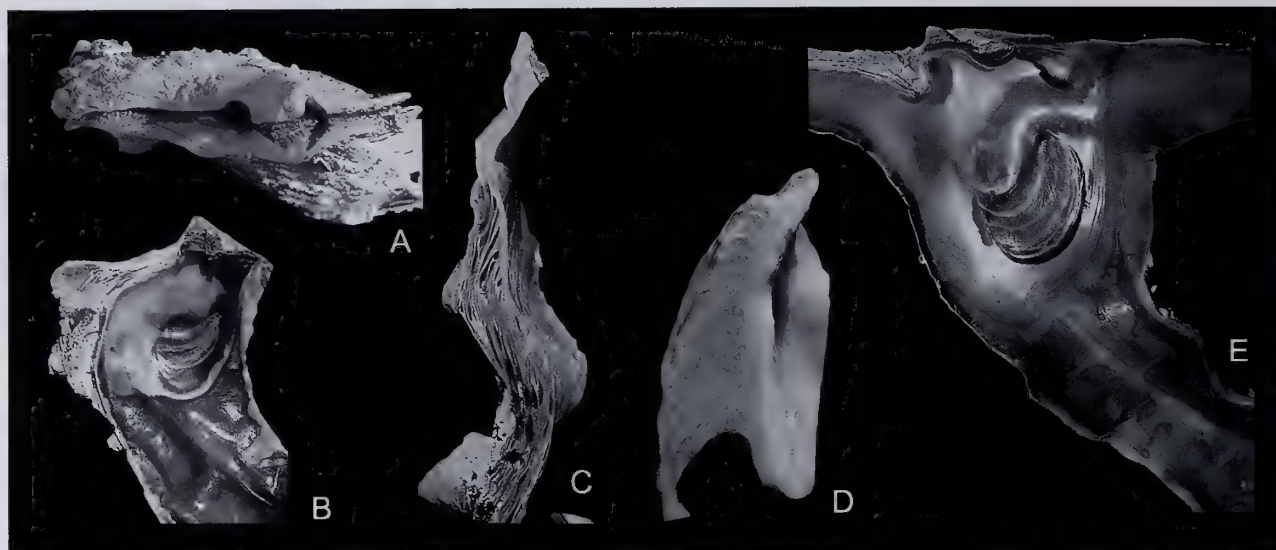
It is difficult to imagine an evolutionary pathway leading from typical *Botula* to *B. hortensis*. Therefore, it is legitimate to suspect that the morphological similarity of this species with *Botula* is due to convergence rather than

phylogenetic affinity (i.e., that *B. hortensis* is not a true *Botula*), or alternatively, that the life habits of *Botula* in the past were substantially more varied than those of Recent species.

**Gastrochaenidae.**— This family contains rock and dead-coral borers, as well as several taxa that evolved secondarily into tube dwellers in soft sediments (Carter, 1978, Savazzi, 1982a, 1999b; Morton, 1983). The boring representatives secrete a calcareous lining onto the inner walls of the borehole, and can extend this lining into a chimney-like projection when threatened by the overgrowth of encrusting organisms. The lining is also functional in protecting the bivalve when it becomes partly exposed. This lining became a stepping-stone to the evolution of the tube-dwelling habit, in which the bivalves are encased in a calcareous envelope, or crypt (Savazzi, 1982a).

Freneix and Roman (1979) illustrated Tertiary echinoids containing the calcareous linings of gastrochaenids boreholes, and interpreted this as an instance of parasitism by the bivalves. However, an analysis of this instance shows that the echinoids most likely were dead at the time of boring, and that the bivalves utilised the test as a substrate. In fact, none of these echinoids visibly reacted to boring by the bivalves, which often passed through the test and built calcareous canopies on both its internal and external surfaces. This lack of a reaction is highly unlikely in a living echinoid, since its test is a porous dermaskeleton containing abundant living tissues. Savazzi (1982a, fig. 3E) il-





**Figure 2.** A–B. *Malleus anatinus* (Gmelin), Recent, Cebu Island, the Philippines. Dorsal view with byssal gape (A,  $\times 1.2$ ) and interior of dorsal portion of right valve (B,  $\times 0.7$ ). C, E. *Malleus malleus* (Linnaeus), Recent, Cebu Island, the Philippines,  $\times 1$ . Interior of right valve of subadult specimen, not yet showing the secondary shrinkage of mantle tissues (see the text for details). D. Unidentified malleid, Middle Eocene, Verona, Italy,  $\times 4$ .

illustrated a comparable instance of a gastrochaenid boring in the test of a Recent sand dollar (also dead at the time of boring), and building calcareous canopies on both sides of the thin echinoid test (in the illustrated specimen, the test was subsequently destroyed by erosion, leaving an isolated crypt).

**Malleidae.**—Typical malleids are epibyssate forms. They are characterised by a monovincular resilium, a byssal notch located close to the umboes (Figure 2A), and in several genera by projections of the shell that function as a stabilising surface in connection with an epibyssate or reclining habit (e.g., Figure 2E; Seilacher, 1984). Yonge (1986) described *Malleus* as a semi-infaunal orthothetic form, but the writer's field observations on living *Malleus* in the Philippines confirm Seilacher's interpretation of this genus as an epifaunal recliner. In malleids, the organism often displays a determinate growth pattern, in which the mantle first grows to the full extent of the shell perimeter in order to build the projections along the edge of the shell, and subsequently shrinks to a substantially smaller area of the inner shell surfaces, leaving behind growth lines on the abandoned inner shell surfaces that allow one to detect the stages of this growth process (leftmost region of Figure 2B).

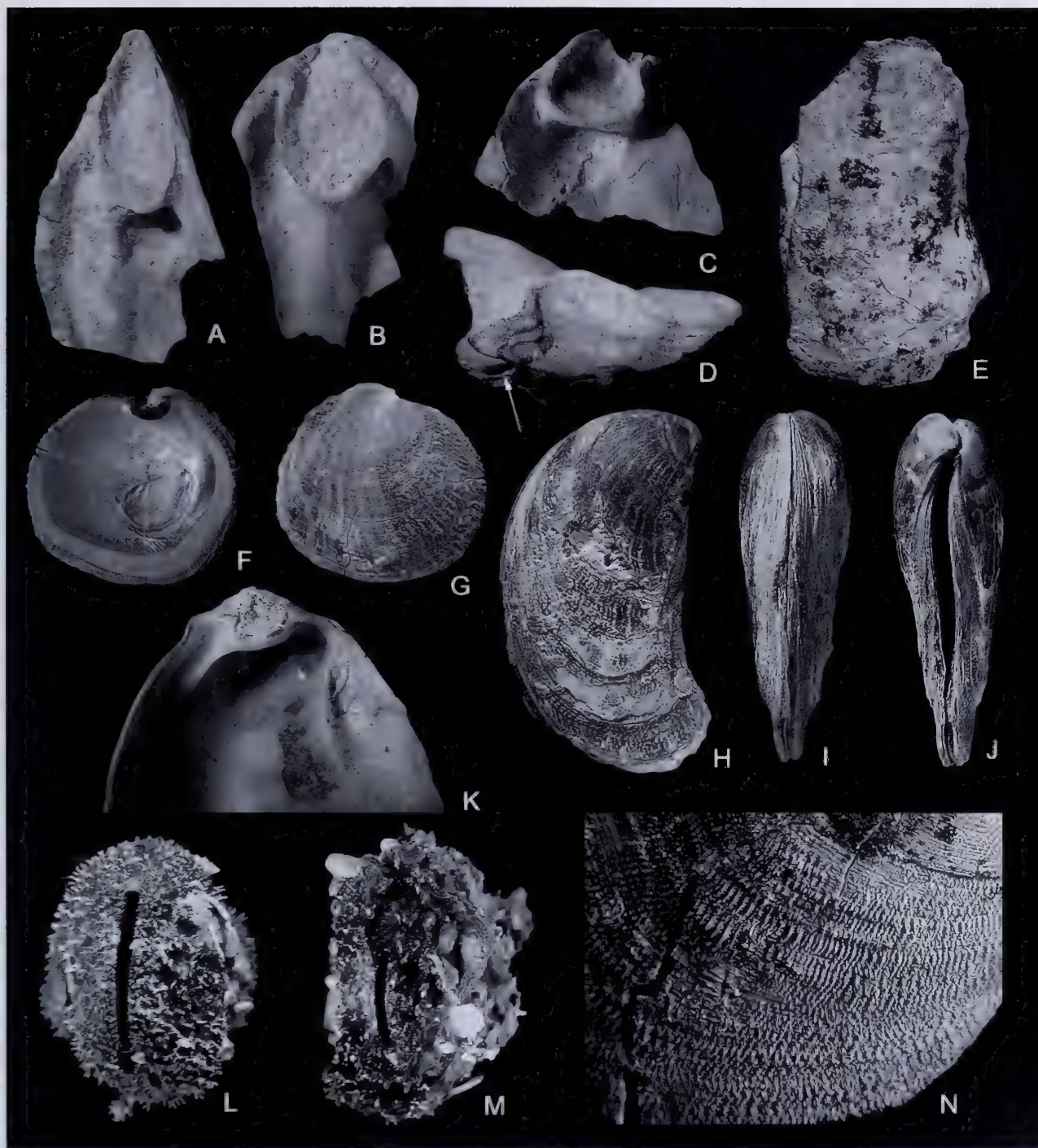
The genus *Vulsella* (Figures 1D, 3F–N) is a malleid endosymbiont in soft sponges (e.g., see Reid and Porteous, 1978, and references therein). The shell is completely embedded in the sponge tissues, and only a short length of the ventral commissure communicates with the external environment (Figures 1D, 3L–M). This genus does not display the shrinking of the mantle tissues in the adult stage displayed by other malleids. The proportions of the shell and its outline are very variable, as a result of irregular growth of the host sponge. Shell height can reach about 100 mm in

the largest specimens, but is usually limited to 30–40 mm.

As verified in living specimens of *V. vulsella* from Cebu Island, the Philippines, the region of exposed commissure is the site of an inhalant water current (Figure 1D). There is, however, no detectable exhalant current along the exposed commissure or the surrounding sponge surface. By letting the bivalve inhale pigment dissolved in sea water, it was found that the sponge tissues facing the posterior commissure of the bivalve (which is deeply embedded within the sponge) absorbed the pigment. Further observation of the sponge in this region showed that it contains numerous openings connecting the postero-dorsal commissure of the bivalve with the canal system of the host. Therefore, *Vulsella* exploits the host sponge as a sink for its exhalant current, and probably takes advantage of the passive flow induced within the sponge canal system by surrounding water currents, in a manner closely similar to that described by Savazzi (1996, 1999a) for the gastropod *Siliquaria*. This flow may reduce the energy expended by the bivalve to strain water. The sponge may gain from the symbiotic association in that the bivalve shells provide a rigid internal framework that allows the sponge to extend in height (Reid and Porteous, 1978). Empty shells of *Vulsella* completely embedded within the sponge are common.

The outer surface of the shell in *Vulsella* bears a sculpture of sharp frills directed obliquely outward (Figure 3N). This sculpture is likely adaptive in greatly increasing the adhesion of the shell to the tissues of the host. It is delicate and always worn away in dead shells found loose on the bottom. Therefore, it is unlikely to be preserved in fossils. The sculpture is prominent in the juvenile stage, and becomes irregular and subdued in the adult stage. This is consistent with the above functional hypothesis, since juveniles are





**Figure 3.** A-E. Unidentified malleid, Middle Eocene, Verona, Italy. Resiliifer and double buttress (A-C,  $\times 2$ ; C is viewed from an oblique left-ventral direction), byssal notch (indicated by arrow, D,  $\times 3$ ) and bivalved specimen lacking the hinge region (E,  $\times 0.7$ ). F-N. *Vulsella vulsella* (Linnaeus), Recent, Cebu Island, the Philippines. Interior and exterior of right valve of juvenile (F-G,  $\times 2.5$ ), exterior of adult (H-J,  $\times 1.3$ ), interior of hinge region of right valve (K,  $\times 2.5$ ), ventral commissure of living specimens in host sponge, probably *Ricinia* sp. (L-M,  $\times 2$ ) and detail of sculpture on exterior of juvenile shell (N,  $\times 10$ ).



less deeply embedded within the sponge, and more likely to be broken loose.

The biomechanics and geometry of the shell in *Vulsella* suggest criteria applicable to detect comparable life habits in fossil forms. The resilium of *Vulsella* is unusually large (Figure 3F, K), and grows proportionally larger with age. By comparison, much larger epifaunal forms like *Malleus* have proportionately smaller resilia (Figure 2B, E), in spite of their much thicker and heavier shells. In *Vulsella*, the large resilium is probably related to the fact that the valves must open against the pressure exerted on the shell by the tissues of the host sponge. As a consequence, the resilium in adult *Vulsella* is inserted onto a well developed and thick resilifer, which displaces the ligament ventrally to the hinge line (Figure 3K). The resilifer is almost absent in juveniles (Figure 3F), and the resilium at this stage is inserted close to the hinge line. The shell wall near the resilifer in adults is strengthened against flexing by a buttress deposited onto the inner shell surface (Figure 3K). This buttress, which is absent in juveniles, is located near the anterior side rather than in a medial position.

The buttress, together with the strong resilium and a somewhat thickened dorsal shell region, stiffens this part of the shell. As a result, the ventral commissure closes thanks to the thinner central region of the shell flexing under the contraction of the adductor muscle. This results in closure of the exposed ventral shell gape. A permanent gape remains along the anterior shell margin (which is embedded within the sponge, and stiffened by the nearby buttress). Reid and Porteous (1978) reported the presence also of a posterior gape, but this feature is absent or reduced in the material available to the writer, especially when the valves are adducted and the ventral gape closed. Thus, it appears that the main function of the resilium is to open the valves progressively during growth, in order to allow further shell growth along the ventral margin.

Most fossil malleids were undoubtedly epibyssate or recliners (see Hertlein and Cox, 1969; Seilacher, 1984). A few forms, however, are similar in general shell morphology to *Vulsella*. In particular, the African Cretaceous *Stefaniniella* (Figure 1E) is comparable in general shape, but has a zigzag postero-dorsal commissure and a larger size (Tavani, 1941, and references therein; Hertlein and Cox, 1969). The inner shell surface of this genus is characterised by a large resilifer, a roughly medial buttress connecting the resilifer to the shell, and a series of septa spanning the space between resilifer and shell surface in the posterior region (Figure 1E). Tavani (1941) regarded such a chambered structure as absent in the Malleidae, and placed this genus in the separate family Stefaniniellidae, but subsequent authors placed it in the Malleidae.

An imperfectly known, unidentified form from the Middle Eocene of Italy (Figures 2D, 3A–E) is similar to *Stefaniniella* in its relatively large size (estimated to about 150 mm in shell height), large resilifer, and septa connecting the resilifer to the shell (Figure 2D). However, its posterior commissure is apparently straight like *Vulsella*, and unlike *Vulsella* and *Stefaniniella* it possesses two buttresses (Figure 3A–C). The buttresses have a massive internal structure, and surround the central septate region on either side. Unlike both

*Vulsella* and *Stefaniniella*, this form also displays what appears to be a well developed byssal notch (arrow in Figure 3D). Unlike in epibyssate malleids (cf. Figure 2A), this notch continues in the ventral direction into an extensive permanent anterior gape, which does not agree well with an epibyssate habit in shallow water. It is possible, instead, that this permanent gape was embedded within a sponge, like *Vulsella*. It may be noted that also in *Vulsella* the anterior gape appears to be delimited dorsally by a vestigial byssal gape. A comparable habit is also possible in *Stefaniniella*, although it is difficult to decide whether this genus possessed a permanent commissural gape. By analogy with *Vulsella*, the exhalant current in *Stefaniniella* would have exited in correspondence with the zigzag portion of commissure. The distinctive zigzag folding of this region of commissure could be an adaptation for increasing stiffness of this shell region.

The Eocene malleid *Euphenax* possesses a lightweight shell with a cavernous outer layer and a chambered inner layer (Hertlein and Cox, 1969). Therefore, a septate or vacuolar structure is not unique to *Stefaniniella* and related genera. Such a structure is also found, for instance, in *Malleus* (Figure 2C). The shell of *Malleus* and related forms displays several constructional elements shared by *Vulsella*, *Stefaniniella* and the Eocene form discussed above. However, these elements are placed in different positions, and their mechanical effects are therefore different. For instance, the adductor muscle in *Malleus* is located close to the hinge (Figure 2B, E), the vacuolar structure is distributed along the height of the shell with the exception of its dorsal region (Figure 2C), and a buttress-like dorso-ventral ridge stiffens the inner side of the shell, but is located ventrally to the adductor muscle, rather than immediately below the resilium (Figure 2B, E). A true resilifer differentiated from the hinge line is also absent in *Malleus*. All these characters are related to an epifaunal life habit, in which the shell is stiff and opens by flexing the resilium, which does not need to be overly large and therefore allows a placement of the adductor muscle not far from the hinge. Finally, the byssal gape in *Malleus* and related forms is well developed, but clearly delimited from the rest of the commissure (Figure 2A), which shows no other permanent gapes.

*Pteriidae*.—*Crenatula modiolaris* is a Recent pterioid byssally attached to soft sponges and covered by a thin layer of sponge tissues (Figure 4A–F). The writer observed living *C. modiolaris* in Bantayan Island, the Philippines, and preserved specimens of *C. nakayamai* in museum collections. Unlike *Vulsella*, this species is not deeply embedded, and its shell morphology is therefore relatively unspecialised with respect to epibyssate pterioids. Unlike in epibyssate forms, its shell is often irregular and visibly distorted. Epibyssate forms can be of variable morphology, as a result of different current regimes, but their shell geometry is rarely distorted. This difference is potentially useful in detecting similar habits in fossils. Crevice-dwelling pterioids are also irregular, but in a different manner. For instance, in the latter it is often possible to recognise in the shell morphology irregularities of the substrate to which the shell had to conform. In *Crenatula*, instead, the contours and surfaces are smooth and often characteristically bulging outwards in





**Figure 4.** A-F. *Crenatula nakayamai* Kuroda & Habe, Recent, Amami-Oshima Island, Kagoshima Prefecture, Japan (Sakurai collection, National Science Museum, Tokyo, Japan). Dried specimens embedded in host sponge, probably *Haliclona* sp. (A, approximately  $\times 1.2$ , B, approximately  $\times 2$ ), isolated shells (C-E, approximately  $\times 1.6$ ), and interior of right valve showing the curved hinge line (F,  $\times 1.8$ ). G-H. *Pterelectroma zebra* (Reeve), Recent, Nagai, Kanagawa Prefecture, Japan (Sakurai collection, National Science Museum, Tokyo, Japan). Left (G,  $\times 5$ ) and right (H,  $\times 5$ ) valve of the same specimen.

a balloon-like fashion (see especially Figure 4E). This irregularity may extend to the ligamental area, which may be bent (Figure 4F). In the long run, this situation is incompatible with further growth, because a bent hinge line prevents the valves from opening gradually during growth, in order to

allow the ventral margins to be extended. The thin shell flexes under the contraction of the adductor muscles, and this allows the bivalves to close the ventral commissure even though the hinge line is curved.

The coating of sponge tissues in *Crenatula* may deter



some predators. However, Reid and Porteous (1978) reported that *Octopus* often predate on *C. modiolaris*. There seems to be no possibility for the exhalant current of the bivalve to be led into the canal system of the sponge, since the whole commissure of the bivalve is exposed, except for the hinge and byssal gape. It is possible that the encrusting sponge is effective as visual camouflage against other predators, since the shell colour of *C. modiolaris* always matches that of the associated sponge, which ranges from light brown to almost black (pers. obs. in Bantayan Island, the Philippines). There is no apparent advantage for the host sponge.

Several pteridi are epibyssate on soft corals or other organisms. *Pterelectroma zebra* possesses an unusual colour pattern (Figure 4G–H) that mimics the hydrozoan substrate. This pattern appears to constitute a visual camouflage (see also Seilacher, 1972, fig. 7G, 10). The fact that this pattern is different on opposite valves (Figure 4G–H) contributes to this function, since an observer sees the pattern on both valves simultaneously through the highly translucent shell. This further hides the shell outline and makes it merge visually against the hydrozoan substrate. Since this specialised colour pattern would not be effective against a different substrate (e.g., rock), it is of potential usefulness as an indicator of symbiotic habits.

**Ostreidae.**—The Recent *Ostrea permollis* is embedded within soft sponges, in a manner comparable to *Vulsella* (Forbes, 1964, 1966). This bivalve is smaller than *Vulsella* (up to about 25 mm in shell length), and its mantle margins and conchiolin are bright yellow like the surrounding sponge tissues. The shell displays no attachment scar. *O. permollis* grows normally when raised in the laboratory in the absence of a host sponge, and the stomach contents in field-collected specimens consist of phytoplankton (above references). A large sponge may contain hundreds of symbiotic oysters, often stacked parallel to each other in especially crowded areas. The inhalant region of commissure is exposed, while the exhalant current is funnelled into canals of the sponge interior.

The adaptive significance of this association is probably protection from predators for the oyster, and, for the sponge, achieving a stiffening structure without spending energy for its construction (Forbes, 1964, 1966). However, the above authors reported that empty oyster shells, although frequent in the outermost layers of sponge tissues, are absent from its centre. The oyster may additionally profit from passively induced flow within the canal system of the sponge. Therefore, this case can be regarded as convergent with *Vulsella*.

**Pectinidae.**—The Recent pectinid *Pedum* (Figure 5A–E) is a nestler in living scleractinian corals (Yonge, 1967; Savazzi, 1998). It settles on the surface of the coral, and it becomes gradually embedded by growth of the host (Figure 5A, B). This genus does not abrade the substrate (except to a very limited extent, see Savazzi, 1998), and both valves are almost flat as viewed in section along the dorso-ventral axis. This is a consequence of the lack of substrate abrasion, because growth of a convex, coiled shell requires the umbones to rotate and move away from each other, thus increasing shell inflation in this area (see Savazzi, 1987). *Pedum* dis-

plays also a very limited amount of ontogenetic migration of the shell toward the surface of the substrate (see the space vacated at the bottom of the coral cavity in Figure 5B). These constraints are reflected in a number of peculiar morphological adaptations, such as the anterior auricle of the right valve being located inside the earlier shell cavity and exposed by secondary resorption of the shell wall (Figure 5C). An inequivalve condition is a further consequence of this mode of growth (Figure 5D, E).

The inability to remove any substantial volume of substrate forces the juvenile to gape broadly (Figure 5A), in order to maintain a cavity in the substrate large enough to accommodate the adult hinge region, which, in turn, becomes laterally asymmetric in order to allow the smaller left valve to move ventrally during growth, thus reducing the space needed to allow valve opening. In conclusion, the shell geometry and growth process of this genus are explained by its symbiosis with scleractinian coral and by its inability to abrade the substrate. A more detailed analysis of the biomechanics and growth of *Pedum* was provided by Savazzi (1998).

The Recent *Chlamys acroporicola* (Figure 5F, G) nestles among the branches of living ramose scleractinians like *Acropora*. Its shell is often slightly deformed in the adult, because of space constraints. Such deformations, together with the lack of attachment scars (this species is byssally attached) would be recognisable in fossils. However, in this instance there appears to be no indirect way to infer the association of this species with living coral. This habit may explain how the life habit of *Pedum* evolved (Savazzi, 1998).

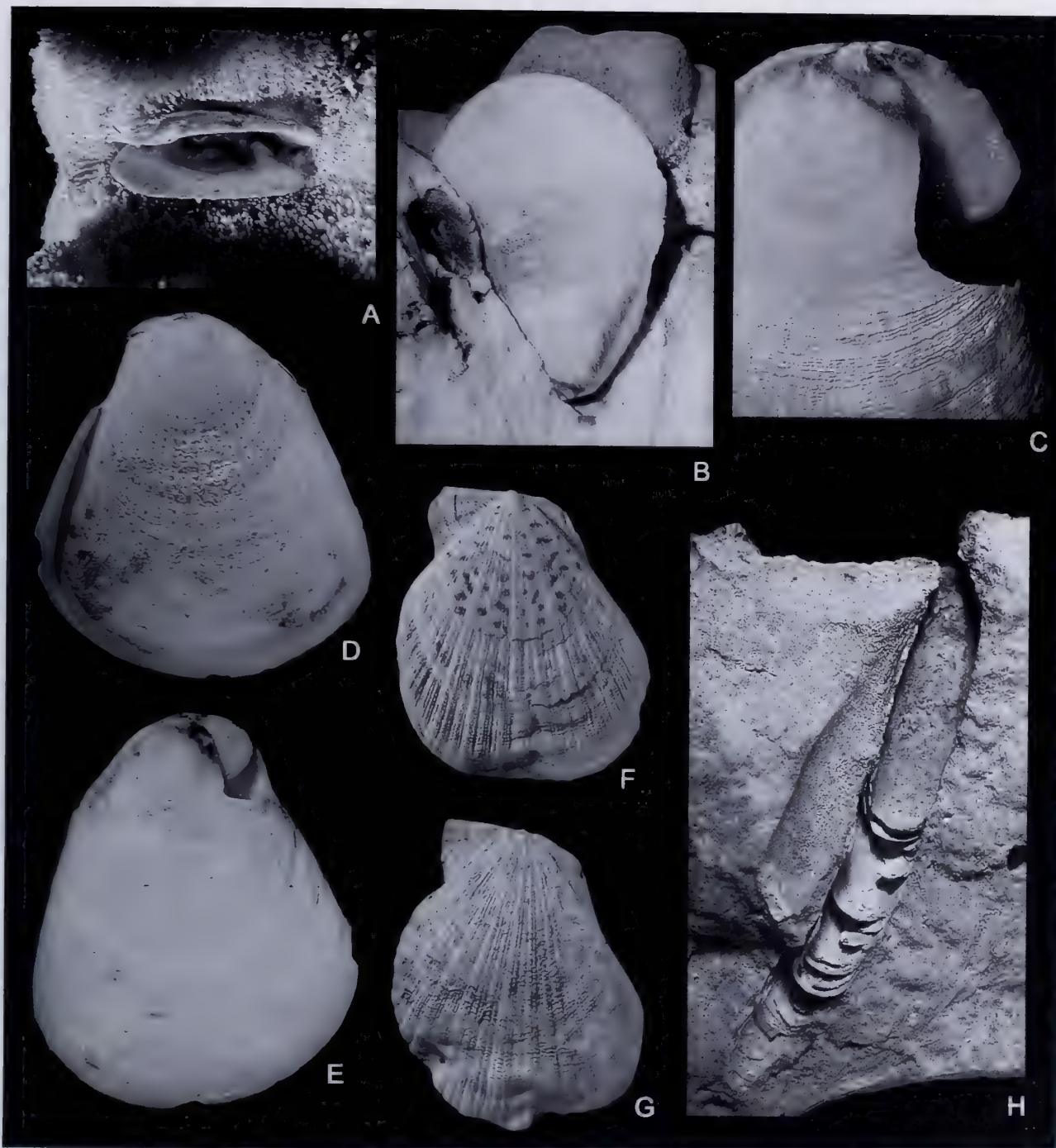
**Carditidae and other nestlers.**—A few other Recent bivalves, like the carditid *Begonia semiorbiculata*, are facultative or obligatory nestlers or borers in scleractinian corals, but their morphology does not seem to be distinctive of these life habits. Several of these forms have been discussed by Savazzi (1999b).

**Other embedded bivalves.**—Several Recent leptonaceans and galeommataceans live within the digestive tract of echinoderms (especially holothurians) and, less frequently, inside the body of other invertebrates (e.g., Voeltzkow, 1891; Malard, 1903; Anthony, 1916; Bourne, 1906). The shell of these bivalves normally shows no morphological adaptation. *Cycladoconcha*, an endoparasite in holothurians, is an exception. The central portion of its shell bears a large hole as a result of secondary resorption (Spärck, 1931), a character potentially recognisable in fossils.

### Ectosymbiotic bivalves

**Unionacea.**—The glochidium of several Recent freshwater Unionacea is an ectoparasite on fishes. Each valve bears a sharp spear along its ventral margin. The tips of these spears converge toward each other, and allow the valves to grip the host like the tips of tweezers when the adductor muscles are contracted (Kat, 1984). The principal adaptive significance of this adaptation is likely that it provides a means for the molluscs to spread upstream along rivers and streams, which would be problematic for bivalves with a planktonic larval stage and a scarcely mobile adult stage. The fossilisation potential of these larval stages is extremely low, so it is not feasible to ascertain directly when





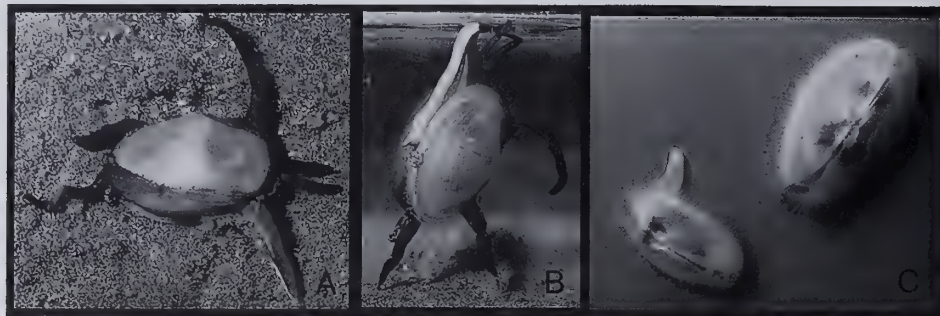
**Figure 5.** A-E. *Pedum spondyloideum* (Gmelin), Recent, Cebu Island, the Philippines. Juvenile (A,  $\times 2$ ) and adult (B,  $\times 1.5$ ) nestling in coral, detail of auricle of right valve (C,  $\times 3$ ), left and right sides of adult (D-E,  $\times 1.4$ ). F-G. *Chlamys acroporicola* (Iredale), Recent, Cabuyan Island, the Philippines,  $\times 2.5$ . H. Borehole of *Lithophaga* sp. originally in a living *Porites* coral, subfossil, Cebu Island, the Philippines,  $\times 1.3$ .

this habit evolved within the superfamily.

*Leptonacea* and *Galeommatacea*.—These bivalves are typically symbiotic with other organisms. A broad range of hosts has been recorded for Recent representatives. They

include crustaceans (especially brachyurans, macrurans, stomatopods and tanaid shrimps), echinoderms (especially holothurians), sipunculids and polychaetes. Association with other organisms (burrowing sea anemones, phoronids)





**Figure 6.** A–B. Living *Scintilla* sp., Cebu Island, the Philippines,  $\times 1.4$ , crawling on sand (A, with the foot lowermost) and climbing the glass of an aquarium (B, with the white sole of the foot visible). C. Two living specimens of *Galeomma* cf. *polita*, Cebu Island, the Philippines,  $\times 3$ . The foot is visible in the lowermost specimen. The anterior inhalant (with larger gape) and posterior exhalant mantle regions are also visible. The shells appear “fuzzy” because they are covered by villous mantle tissue.

has been described as well (e.g., see Fischer, 1930; Ohshima, 1930; Popham, 1940; Caullery, 1952; Boss, 1965; Rees, 1967; Morton, 1980, 1988; Noble *et al.*, 1989). Many of these bivalves are associated with a specific type of host, but exceptions are known. *Mysella bidentata*, for instance, has been observed on a large variety of invertebrates, including annelids, sipunculids and echinoderms (Boss, 1965). Leptonacean and galeommatacean bivalves may be byssally attached to the host, or live in its burrow. Several species have been found nestling among epifaunal bivalves or rock and coral crevices, and their hosts, if any, are unknown.

Some leptonaceans and galeommataceans are free-living, and can use the adhesive sole of the foot to creep, and even to climb (Figure 6). Additional peculiarities are constituted by the mantle often covering totally or in part the outer shell surface, and by mantle tentacles, ranging in number from a few to hundreds, which may be functional as a defence against predators (above references). In these superfamilies, the inhalant current enters the mantle in correspondence with the anterior shell slope, and the exhalant leaves from the posterior. The taxonomy of these groups is difficult, and several species are highly polymorphic.

The Recent galeommatacean *Curvemysella paula* (Figure 7A–D) possesses a conspicuously concave ventral margin and a twisted commissure plane. This peculiar morphology is adaptive: this species is byssally attached to the columella of a gastropod shell inhabited by a hermit crab (Morton and Scott, 1989; pers. obs.). The bivalve is located well within the shell, and invisible from the aperture. The commissure conforms to the geometry of the columella and inner shell surface of the gastropod.

Shell morphology in this species is rather constant, but it is not known whether it is genetically preprogrammed or ecotypically determined by space constraints. The somewhat irregular shape of the byssal gape suggests a morphogenetic programme at least partly controlled by the topography of the substrate. The Eocene sportellid *Hindsiella*, which possessed a comparably concave ventral margin, may have had a similar life habit. Several other representatives display a concave ventral margin. This fea-

ture may be related to byssal attachment to a convex substrate (e.g., exoskeletal surfaces of arthropods). As discussed by Savazzi (1987), this geometry is adaptive in relieving stress on the byssus, and therefore may enhance the adhesion of the organism to the host.

The galeommatacid *Ehippodonta* possesses a shell with a straight hinge line and roughly semicircular and almost flat valves. This genus lives within crustacean burrows, and typically keeps the valves spread apart at an angle of about  $180^\circ$  to each other. The valves cannot be closed and, at maximum adduction, form an angle of roughly  $90^\circ$  to each other. The foot is large, with a wide flat sole used for creeping.

#### *Mysella*, a symbiont on *Lingula*

A Recent galeommatacid (Figure 7E–I), here identified as *Mysella* sp. because of its hinge structure, was observed by Savazzi (1991) byssally attached to the shells of the living inarticulate brachiopod *Lingula anatina* from the Philippines. This seems to be the only literature record of bivalves symbiotic with brachiopods. The constant placement of these bivalves near the anterior commissure of *Lingula* and their apparently obligatory association with the brachiopod suggest a symbiotic association. Subsequent field work by the writer provided the opportunity for a more detailed investigation, and the results are discussed below.

**Material.**—In November, 1994, 141 specimens of *L. anatina* were collected manually by digging out sediment from an area of approximately  $2\text{ m}^2$  on a tidal flat in front of the Poor Clare Monastery, Tayud, Cebu Island, Philippines ( $10^\circ 21' 15''\text{N}$ ,  $123^\circ 59' 15''\text{E}$ ). This is the same locality studied by Savazzi (1991). About 20 specimens carrying attached bivalves were placed in aquaria for observation, while the rest were fixed and dried.

**Observations on *Lingula*.**—Savazzi (1991) reported that *L. anatina* collected in 1990 from the same locality sometimes exceeded 50 mm in shell length. However, in 1994 only 5 specimens in the collected sample exceeded 30 mm, with none reaching 40 mm. A search in the surrounding area failed to produce larger specimens. A subsequent visit in the same locality in 1997 yielded specimens of *L. anatina*



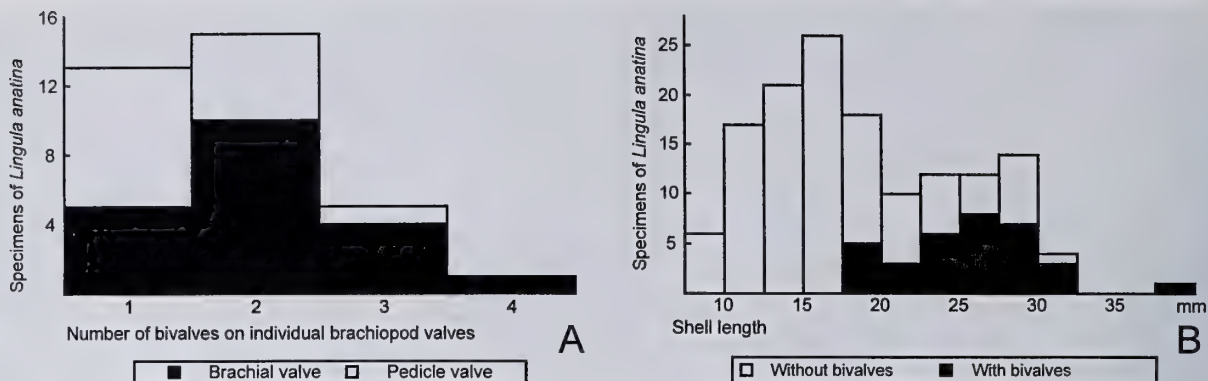


**Figure 7.** A-D. *Curvemysella paula*, Recent, Cebu Island,  $\times 10$ . E-I. *Mysella* sp. on *Lingula anatina*, Recent, Cebu Island, the Philippines. Specimens epibyssate on *Lingula* (E,  $\times 8$ ; F-G,  $\times 5$ , arrows indicate juvenile *Mysella*, small round objects are egg capsules), byssal threads on *Lingula* (H,  $\times 8$ ) and living specimen probing the edge of the *Lingula* mantle with the extended foot (I,  $\times 6$ , arrow indicates the bivalve foot).

never exceeding 25 mm in shell length. In 1997, *Mysella* sp. was absent from this locality and surrounding areas. The local environment may have become gradually less favourable for *L. anatina* because of the construction of numerous dry piers, which restrict water currents, and an increase in pollution. The gradual decrease in size and abundance of *L. anatina* observed in the test locality may be general in Cebu Island. While this species was available on a daily basis in local fish markets until 1990, it was seldom

seen in 1994 and 1997.

**Frequency and distribution of epibionts.**—Several *Lingula* collected in 1990 and 1994 carried byssally attached *Mysella* sp. These bivalves were exclusively found attached to living *Lingula*. No other epibionts were observed on *L. anatina* with the exception of two specimens of the gastropod *Calyptrea* sp., but several specimens of *Lingula* carried egg capsules, possibly laid by gastropods (e.g., Figure 7E-G).



**Figure 8.** A. Distribution and clustering pattern of *Mysella* sp. on right and left valves of *Lingula anatina*. B. Size distribution of *Lingula anatina* specimens with and without attached *Mysella*.

*Mysella* sp. is attached indifferently on either valve of the brachiopod (Figure 8A). However, only one specimen of *L. anatina* carried individuals of *Mysella* sp. on both valves. As shown in Figure 8B, the size-distribution of the sample of *L. anatina* is visibly bimodal, with a single outlier at the extreme right of the histogram suggesting a third peak. These peaks likely correspond to year classes. If so, they indicate a rather high yearly mortality (roughly 50% from year 1 to 2, much higher from year 2 to 3). *Mysella* sp. shows a clear preference for larger hosts: 53% of the specimens of *L. anatina* above 20 mm in shell length carry one or more attached *Mysella* sp., while only 5.7% of the specimens below 20 mm do. In total, 23.4% of *L. anatina* carry bivalve commensals. 37 specimens of *Mysella* sp. were collected in total.

Most specimens of *L. anatina* carry one or two bivalves, with a single specimen carrying four (of which one is a small juvenile; Figure 7F). When two or more individuals are present, they usually forms tight clusters. This pattern may result from a preference by *Mysella* sp. to attach near an already present individual, as shown by the different sizes of individuals within the same cluster (Figure 7E-G).

In several cases, the bundle of byssal threads by which *Mysella* sp. is attached to the host continues posteriorly into a trail of old, severed byssal threads (Figure 7G, H). This trail is apparently produced by the migration of *Mysella* sp. toward the anterior commissure of its host. Since *Mysella* sp. is invariably located close to the anterior commissure of *L. anatina* (see also below), this migration must be a response to growth of the brachiopod shell. *Mysella* sp. is preferentially attached in correspondence of the inhalant currents of the host, which enter the shell along the lateral regions of the anterior commissure (see Chuang, 1956; Rudwick, 1970; Savazzi, 1991; and references therein), rather than in correspondence with the centrally located exhalant current.

The shell of *Mysella* sp. is antero-posteriorly elongated, with a straight or slightly concave ventral margin. The umbones are slightly opisthocline and opisthogyrate, and located slightly posterior to the midlength of the shell. The anterior shell slope is slightly more developed than the pos-

terior, which is somewhat truncated. The ventral shell margin is straight or slightly concave, with a thickened shell edge. The periostracum on the outer shell surface is thick and dark brown in colour, and forms a thick carpet of short periostracal shingles arranged in radial lines.

The hinge shows a well developed, elongated anterior tooth and a somewhat shorter posterior tooth on the right valve. The left valve shows corresponding sockets, delimited ventrally by anterior and posterior teeth shorter than in the opposite valve. The ligament consists of a resilium located immediately below the umbones and inserted onto the shell within a depressed ligamental pit. The resilium has a roughly circular median section and is arcuate in antero-posterior view, with the convexity on its ventral side. This suggests that some flexing, in addition to compression, is involved in its function. The ventral side of the ligament bears a central calcified patch, white in colour, on its ventral surface. This is not a true ossiculum or lithodesma, because it does not have well defined edges and cannot be isolated from the rest of the ligament by maceration in alkali (when this was attempted, the calcified patch invariably disintegrated into its constituent aragonitic crystals).

The anterior adductor muscle scar is located in a rather dorsal position, while the posterior is displaced ventrally and close to the posterior shell margin. The area of the anterior adductor scar is substantially larger than that of the posterior. The reduced area of the posterior adductor scar, compared to its anterior counterpart, may be related to the fact that the displacement of the posterior adductor in the ventral direction results in an increase in length of the lever-arm acted upon by this muscle, which in turn lessens its strength requirements. The anterior pedal retractor scar is adjacent to the anterior adductor scar, while the posterior pedal retractor scar is well separated from the corresponding adductor scar, and located more dorsally. This separation is likely a consequence of the unusual placement of the posterior adductor (see above).

The ventral displacement of the posterior adductor muscle (see above) is infrequent in bivalves, and reduces substantially the length of posterior commissure available to the respiratory current(s). However, the posterior commissure in



*Mysella* houses only the exhalant current, thus reducing the need for an extensive length of commissure to keep the inhaled and exhalant currents separate in the lack of siphons.

When *Lingula* is in life position with the anterior region of the commissure uppermost (see Savazzi, 1991, and references therein), the posterior region of *Mysella* sp. does not face upwards, unlike what was reported by Savazzi (1991). Instead, it is directed downwards. Thus, the life orientation of *Mysella* sp. is essentially the opposite of typical infaunal bivalves.

In the laboratory, *Mysella* sp. is inactive for most of the time. At intervals of several minutes, the anterior commissure of *Mysella* sp. gapes, and the foot is extended toward the anterior commissure of the host. The tip of the foot probes several times in quick succession on the basal region of and between the brachiopod setae (Figure 7I), and is subsequently retracted within the shell. The process lasts 1–2 seconds, may be repeated 2–3 times in succession, and is followed by another period of inactivity. The foot was never extended into the mantle cavity of the host, and the probing activity caused no visible reaction by the brachiopod. On the other hand, artificial stimulation of the setae and mantle of the brachiopod with a flexible bristle in the same region touched by *Mysella* sp. caused an immediate valve-adduction by the brachiopod. The setae, mantle tissues and shell margin of *L. anatina* in proximity of attached *Mysella* sp. showed no visible damage or alteration.

After spending a few hours in aquaria, a few specimens of *Mysella* sp. detached from their host and started to move about epifaunally. Locomotion consists of a forward extension of the foot, adhesion of its tip to a solid object, followed by retraction of the foot, which causes the shell to be dragged forward. The tip of the foot readily adheres to smooth glass surfaces. No burrowing activity was observed, and detached individuals did not reattach to any of the brachiopods placed in the aquaria.

Four preserved specimens of *Mysella* sp. were dissected and their guts examined. They were found to be empty or to contain small amounts of matter, the nature of which was not recognisable under an optical transmission microscope or a dissecting microscope.

**Significance of association between *Mysella* and *Lingula*.**—*Mysella* sp. likely feeds on mucus and/or on detritus trapped in mucus secreted by *L. anatina*. As described above, the tip of the foot is adhesive, and likely used to collect food particles from the mantle and setae of the host. This feeding activity causes no detectable damage to the host, and might aid in its cleansing. This is apparently the first time the feeding of a galeommatacean on its host was observed.

The preferential placement of *Mysella* sp. near the inhaled currents of *L. anatina* is adaptive in this context. The faeces of *L. anatina* are a potential source of food for a symbiont, but faecal pellets are projected into the water column by quick contractions of the brachiopod valves (above references), and therefore may be difficult or impossible to exploit by an organism attached to the outside of the *Lingula* shell.

The shells of *Mysella* sp. byssally attached on *L. anatina* may hinder or prevent the host from reburrowing when it becomes exposed by sediment erosion. In this situation, it is

possible that *Mysella* sp. detaches itself from exposed *Lingula*, as observed in the laboratory, or becomes dislodged by the energetic burrowing movements employed by *Lingula* (see Savazzi, 1991). It is also likely that *Mysella* sp. hinders the vertical movements of *L. anatina* within its burrow (see also below). A few of the specimens of *L. anatina* showed tufts of byssal threads produced by individuals of *Mysella* sp. that subsequently detached (Figure 7H). The distance of some of these tufts from the anterior commissure of *L. anatina* shows that the brachiopod shell grew substantially after the bivalve detached.

The clustering of *Mysella* sp. provides no obvious advantage in feeding, since adjacent bivalves must then share the same region of host commissure. Rather, it is possible that clustering of *Mysella* sp. makes their individual shells less likely to be dislodged by the movements of *Lingula* within its burrow. This may be especially true of small individuals of *Mysella* nestling close to adult ones (arrows in Figure 7E, F).

The morphology of the burrows of *L. anatina* carrying *Mysella* sp. was observed in three instances. These burrows show a larger diameter and an irregular cross-section in correspondence of the epibionts. These irregularities are potentially preserved in fossilised burrows of linguliform brachiopods (e.g., *Lingulichnites*, see Szmuc *et al.*, 1976). The existence of a comparable association between extinct inarticulate brachiopods and external symbionts, therefore, could be detectable from trace fossils.

### Bivalves as hosts to macrosymbionts

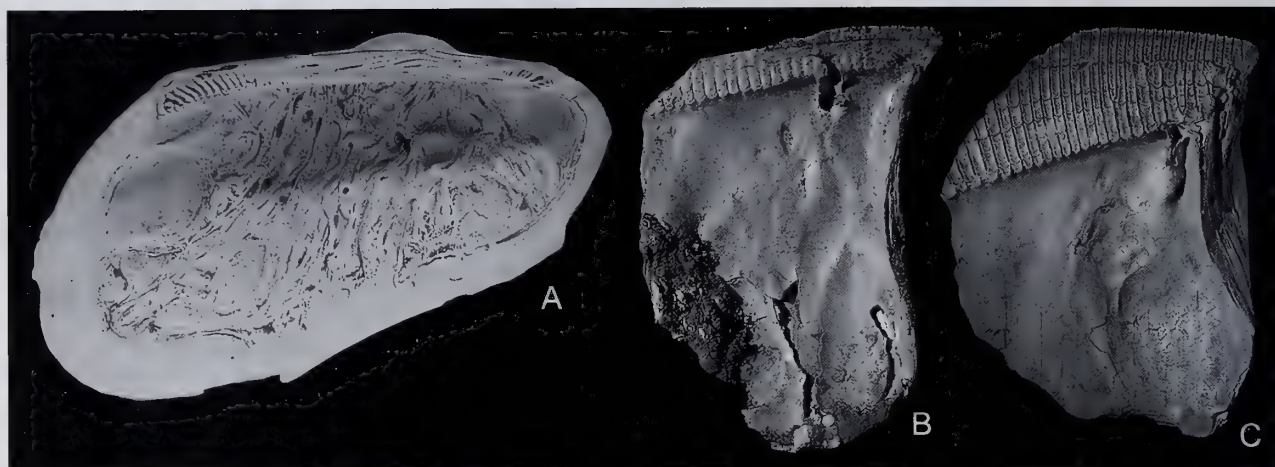
The internal surfaces of bivalve shells occasionally display teratological characters produced by worm-shaped organisms living within the mantle or between the mantle and the inner shell surface (Figure 9). These endosymbionts are likely parasites, because the bivalve host is visibly damaged, and likely receives no advantage from the association.

In some Triassic localities of NE Italy, most specimens of megalodontid bivalves display a U-shaped furrow within one valve (or, more rarely, one such furrow in each valve), with the bottom of the U in proximity to the apex (pers. obs.). A comparable type of infestation was described in Pliocene *Isognomon* (Figure 9B, C; Savazzi, 1995). In this case, the parasite body, as outlined by secondary shell secretion of the bivalve, often spanned across the hinge and followed a twisted and snaking pathway along one or both valve interiors. In two specimens, this induced the formation of a teratologic lithodesma, a feature which is absent in normal shells of all representatives of this family, but present in taxonomically unrelated bivalves (above reference).

In a specimen of the Pliocene arcid *Barbatia mytiloides*, tens of parasites were inhabiting the space between mantle and shell (Figure 9A; Savazzi, 1995). It is interesting to note that the parasite did not spread to the myostraca, a situation which probably would have resulted in the death of the host, and that all parasites eventually were sealed off by the bivalve. A morphologically identical reaction to a parasite is observed also in Recent *Scapharca* from Japan (pers. obs.).

It is usually infeasible to decide the nature of these symbionts in fossil material, since their traces on the bivalve





**Figure 9.** Interior of right valves of bivalves parasitised by worm-like organisms. **A.** *Barbatia mytiloides* (Brocchi), Middle Pliocene, Piacenza, Italy,  $\times 1.2$ . **B-C.** *Isognomon* (*Hippochaeta*) *maxillatus* (Lamarck), Upper Pliocene, Asti, Italy,  $\times 0.4$ .

shells reveal no morphological features, except the general body shape and size of the symbiont.

Both boring and tube-building polychaetes are frequent on the external surface of bivalve shells, and their distribution provides information on the life orientation and life habits of the hosts. In particular, in semi-infaunal bivalves the presence of polychaetes indicates that the shell region they inhabited was exposed above the surface of the sediment. Usually it is not possible to decide whether these polychaetes are true symbionts (frequently, they may settle on a variety of different substrates and organisms). The preferential settlement of semi-endolithic polychaetes in proximity of the exhalant region of commissure of nonsiphonate bivalves (e.g., Arcidae, pers. obs.), however, suggest that they exploit the faeces and/or pseudofaeces of the bivalve as a food source.

### Concluding thoughts

Photosymbiosis has been proposed to explain the large size and/or unusual shell thickness of several fossil bivalves (see above). However, the Tridacnidae are the only Recent bivalves complying with this interpretation. All other documented cases of Recent photosymbiotic bivalves are small forms and, except for *Corculum*, virtually nothing in their shell morphology suggests photosymbiosis.

Stable-isotope analyses could be used to prove photosymbiosis in fossils. This method assumes that the stable-isotope composition of the shells of bivalves housing photosymbionts differs from those of conventional bivalves, since a substantial portion of the carbonate found in the tridacnid shell originates from the photosymbionts. However, with the exception of the Tridacnidae, all Recent photosymbiotic bivalves studied in this respect show isotope profiles similar to those of nonphotosymbiotic forms (above references). In most cases, therefore, proving (or disproving) reliably instances of photosymbiosis in fossil bivalves is

not possible at present, unless photosymbiosis is reflected in morphological adaptations that cannot be explained by other adaptive contexts.

Chemosymbiosis in fossils is even more difficult to prove than photosymbiosis. The only reliable method is probably the study of ichnofossils, especially if associated with specimens preserved in the life position. It may be possible to infer chemosymbiosis in bivalves which, like the Recent *Solemya* and Lucinidae, build specialised feeding burrows with canals that reach deep within the anoxic sediment.

Macrosymbiosis has a better potential than micro-symbiosis of being recognised in fossil material, especially if the associated organisms are preserved. It is usually possible to decide, for instance, whether scleractinian coral was dead or alive at the time it was inhabited by a boring or nestling bivalve. Bivalves that bore in living coral display a range of distinctive behavioural and morphological adaptations to this life habit.

It is more difficult to recognise whether a bivalve was embedded in a sponge or other organism with a low likelihood of being preserved. Specialised life habits like the deep embedding of *Vulsella* and *Ostrea permollis* within sponges can be suspected from the lack of a byssal gape or cementation surface, coupled with a shell morphology and size unlikely for a sessile soft-bottom dweller. A few forms taxonomically related and morphologically similar to *Vulsella* may have had comparable habits in spite of the presence of a byssal notch, since byssal attachment on the surface of a sponge in the juvenile stage may have preceded the embedded adult stage, and the byssal notch may have constituted the morphogenetic "trigger" for the subsequent formation of a broader respiratory gape in the same region of the commissure. The presence of unusually strong hinge structures in otherwise thin shells and of adductor muscle scars unusually (for malleids) displaced toward the ventral region corroborate this idea.

Shallow-embedded pteriids within sponges display a



highly variable shell morphology with distinctively bulging irregularities, also potentially recognisable in fossils. Epibyssate attachment to soft-skeleton coelenterates, on the other hand, does not result in comparable morphological characters.

It is usually difficult to decide from shell morphology alone whether an epibyssate pterid was attached to a living or dead substrate. The cryptic colour pattern of *Pterelectroma zebra*, which provides camouflage against the background of the branched hydrozoan with which the bivalve is associated, seems to be the only exception.

Symbiotic hosts contained within bivalves sometimes can be recognised from teratological reactions of the bivalve. Worms or worm-like organisms living in the mantle cavity, or between the mantle and the shell, often cause recognisable deformation in the shell. Shell-boring or externally cemented polychaetes are usually placed in correspondence to the exhalant current (especially in nonsiphonate bivalves). In addition to allowing one to detect an association between worms and bivalves, these epibionts are useful in helping one to reconstruct the life position of the bivalve with respect to the substrate.

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### **Erratum**

In the Contents on the back cover of Vol. 4, No. 2 and the Contents (p. 314, line 14 from bottom) of Vol. 4, No. 4, the name of the first author of the paper by Hasegawa and Hatsugai was misspelled. Read Takashi Hasegawa for Takeshi Hasegawa.

## A GUIDE FOR PREPARING MANUSCRIPTS

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## 行 事 予 定

- ◎2001年年会・総会は、2001年6月29日（金）、6月30日（土）、7月1日（日）に「国立オリンピック記念青少年総合センター」で開催されます。21世紀最初の年会ですので、「21世紀の古生物学」を統一テーマとし、29日に統一シンポジウム、30日と1日に17件の課題別シンポジウムが行われます。  
一般講演はポスター講演だけに限って受け付けます。口答発表形式による一般講演はありませんのでご注意ください。ポスター講演の申し込み締切日は2001年5月9日（水）です。
- ◎第151回例会は、2002年1月26日（土）、1月27日（日）に鹿児島大学理学部で開催されます。1月27日（日）午後に公開講演として「21世紀は自然史の時代 ―古生物学・フィールド科学からの提言―：世話人、森 啓・矢島道子」を実施致します。一般講演の申し込み締切は11月30日（金）です。
- ◎2002年年会・総会（2002年7月上旬開催予定）には福井県立恐竜博物館から開催申し込みがありました。また、第152回例会（2003年1月下旬開催予定）には横浜国立大学教育人間科学部から開催申し込みがありました。
- ◎古生物学会では、小人数で実施されるワークショップやショートコースを主催しております。学会から金銭を含む援助を行なうことができますので、企画をお持ちの方は行事係までお問い合わせ下さい。

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## THEME ISSUE

### Morphological Approaches in Paleobiology

#### CONTENTS

<b>Takao Ubukata:</b> Morphological approaches in paleobiology .....	1
<b>Enrico Savazzi:</b> Morphodynamics of an endolithic vermetid gastropod .....	3
<b>Kazushige Tanabe, Cyprian Kulicki, Neil H. Landman and Royal H. Mapes:</b> External features of embryonic and early postembryonic shells of a Carboniferous goniatite <i>Vidrioceras</i> from Kansas .....	13
<b>Takenori Sasaki:</b> Macro-and microstructure of shell and operculum in two Recent gastropod species, <i>Nerita</i> ( <i>Theliostyla</i> ) <i>albicilla</i> and <i>Cinnalepeta pulchella</i> (Neritopsina: Neritoidea) .....	21
<b>Takao Ubukata:</b> Geometric pattern and growth rate of prismatic shell structures in Bivalvia .....	33
<b>Richard A. Reyment and W. James Kennedy:</b> Evolution in morphometric traits in North American Collignoniceratinae (Ammonoidea, Cephalopoda) .....	45
<b>Enrico Savazzi:</b> A review of symbiosis in the Bivalvia, with special attention to macrosymbiosis .....	55
<b>Erratum:</b> Article by Takashi Hasegawa and Takayuki Hatsugai in Vol. 4, Nos. 2 and 4 .....	75



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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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# *Hyotissocameleo*, a new Cretaceous oyster subgenus and its shell microstructure, from Wadi Tarfa, Eastern Desert of Egypt

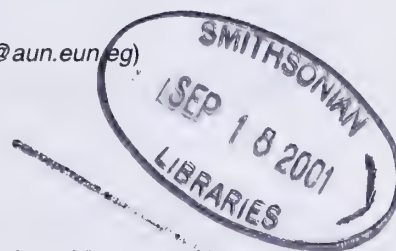
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**Abstract.** On the basis of rib morphology and other characters, *Ostrea tissoti* Peron and Thomas found in Egyptian Campanian sediments is placed in the genus *Cameleolopha* Vyalov, 1936 and the subgenus *Hyotissocameleo* n. subgen. This new subgenus is distinguished from *Cameleolopha* s.s. in having dichotomous to trichotomous round-crested radial ribs, chomata, a long triangular resilifer and a reniform to comma-shaped adductor muscle scar. The main part of the shell shows regularly foliated and in part cross-foliated structure. Neither chalky deposits nor chambers are recorded. Silicification of the original calcitic structure is recognized. Recrystallization and dolomitization resulting from diagenetic processes are observed.

**Key words:** Cretaceous, Egypt, oyster, shell microstructure, systematics

## Introduction

Intraspecific and interspecific variations in shell morphology are both very wide in oysters. This results in the occurrence of confusing homeomorphs at all taxonomic levels in the superfamily and enhances the difficulty of oyster taxonomy. It is essential to study populations rather than individuals for the reliable and accurate identification of oysters (Kassab and Zakhera, 1994, 2000). Dhondt (1985) noted that *Lopha* (*Actinostreon*) Bayle, 1878, *Cameleolopha* Vyalov, 1936, *Nicaiolopha* Vyalov, 1936 and *Acutostrea* Vyalov, 1936, all tend to have homeomorphic shells.

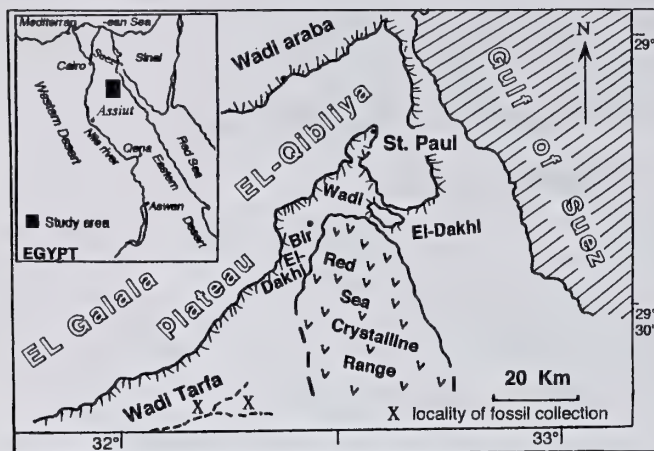
Specimens of "*Ostrea*" *tissoti* Peron and Thomas treated in this paper, were collected from Upper Cretaceous sediments in the northern part of the Eastern Desert of Egypt (Figure 1). This species has been attributed to the genus *Nicaiolopha* Vyalov, 1936 (Kuss and Malchus, 1989; Malchus, 1990). We analyzed its morphology and shell microstructure and reached the conclusion that it belongs to the genus *Cameleolopha* Vyalov, 1936 of the subfamily Lophinae Vyalov, 1936. A new subgenus *Hyotissocameleo* is proposed to accommodate the morphological differences of the species.

## Sample preparation

To facilitate SEM observations of "*Ostrea*" *tissoti*, shells of this species were sectioned in radial, transverse and oblique directions, and parallel to the long axis of the shell. The sectioned surface of each specimen was polished and etched with 0.1 N hydrochloric acid for 20 seconds and then coated with gold for scanning electron microscopy (SEM). Silicified parts and their surroundings have been subjected to microprobe analysis for mineralogical determination.

## Mode of occurrence and taphonomy

A large number of specimens of "*Ostrea*" *tissoti* were collected from yellowish brown, marly mudstone that appears at several Campanian horizons in the Duwi Formation. The oysters occur as articulated and disarticulated valves, arranged parallel to the bedding plane. No preferred orientation of the valves, convex up or down, was observed. The subequal size and thickness of valves may serve to exhibit the differential effect of storms. Several xenomorphs show the oysters lived on a shelly or hard bottom. Spatulate forms with a small attachment area represent a phenotype that lived on a relatively soft bottom.



**Figure 1.** Index map of Wadi Tarfa area, Eastern Desert of Egypt, showing the sampling locality of the Cretaceous oyster.

The presence of few juvenile shells besides those of adults in the same assemblage is indicative of limited or short episodic storm events that caused the shells to form shell-banks. It is very rare to find other bivalves or macroscopic fossils. A low rate of accumulation of muddy clastics allowed the valves to be close to each other, sometimes with the right valves adhering to each other, due to later diagenetic processes.

Silicification and dolomitization during diagenesis are recognized. Silicification affected the calcium carbonate skeletal material, as will be mentioned later, as well as the matrix in which the shells were enclosed. Dolomitization affected only the matrix. The limited dolomitization is indicated by the presence of dolomitic rhombs in the cement between the valves or in sediments filling holes in the shell. The holes are thought to have been formed by dissolution of shell material during the animal's life or shortly after death, but before

consolidation of the enclosing sediments.

### Biometrical remarks

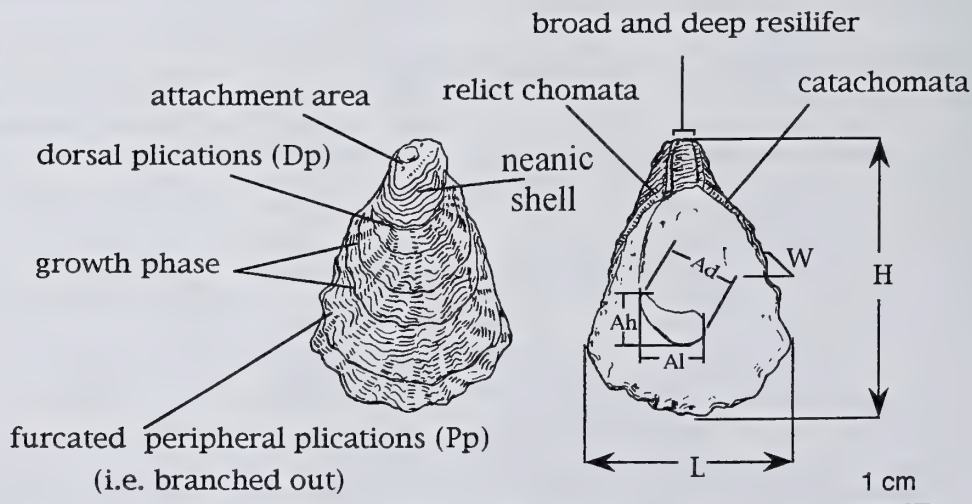
A biometric analysis has been made for individuals of shell height more than 23 mm. Smaller specimens are rare in occurrence. This is probably related to low mortality of the juveniles or presence of some kind of post-mortem sorting and fragmentation of smaller shells. Overall morphology and measurements and the internal architecture of the shell of "*Ostrea*" *tissoti* are diagrammatically shown in Figures 2, 3 respectively.

Although the bivariate scatter diagrams (Figure 4) show weak correlation between pairs of height, length and width, it suggests a large constraint of environmental conditions on shell morphology.

For some individuals the dimensions of the adductor muscle of their right valve are sometimes larger than those of their left valve (Table 1). This is probably related to left valve convexity, which leads to contraction of the size of the muscle pad. When the difference between length of the adductor muscle pad (Al) and the maximum diameter of the adductor muscle pad (Ad) (Table 1) is small, the muscle (by its long diameter) becomes close to perpendicular to the shell long axis, while a greater difference is reflected in a steeper dip to the point that the muscle becomes obliquely vertical (maximum difference). This difference is proportional to the ratio of shell height and length.

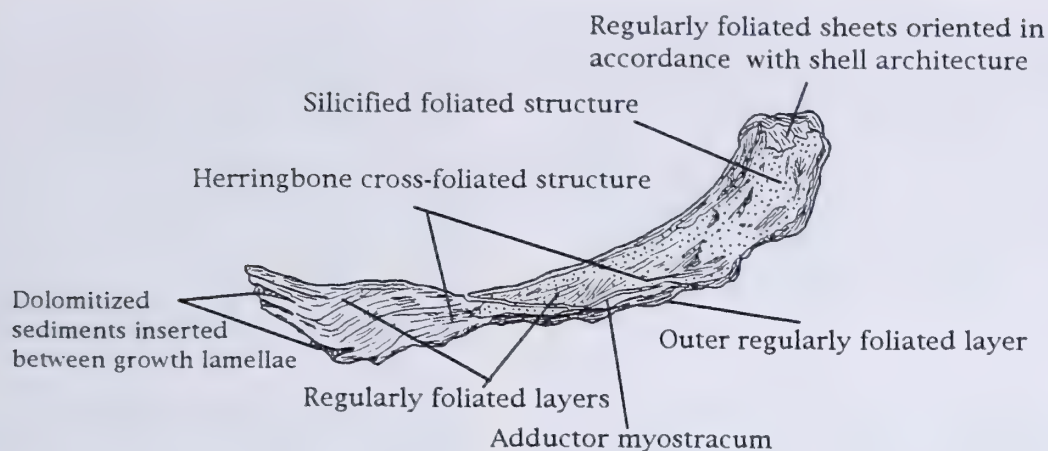
### Shell microstructure

Shell microstructure is important in bivalve systematics (Douvill , 1936; Newell, 1965; Taylor *et al.* 1969; Stenzel, 1971; Waller, 1978; Torigoe, 1981; Freneix, 1982; Dhondt, 1985; Carter 1990; Malchus, 1990; Agrabawi, 1993; Zakhera 1999). The terminology used here follows the descriptive nomenclature outlined by Carter (1990) and Malchus (1990). Stenzel (1971) erected the new genus *Hyotissa* and called it pycnodonteine on the basis of the presence of a vesicular

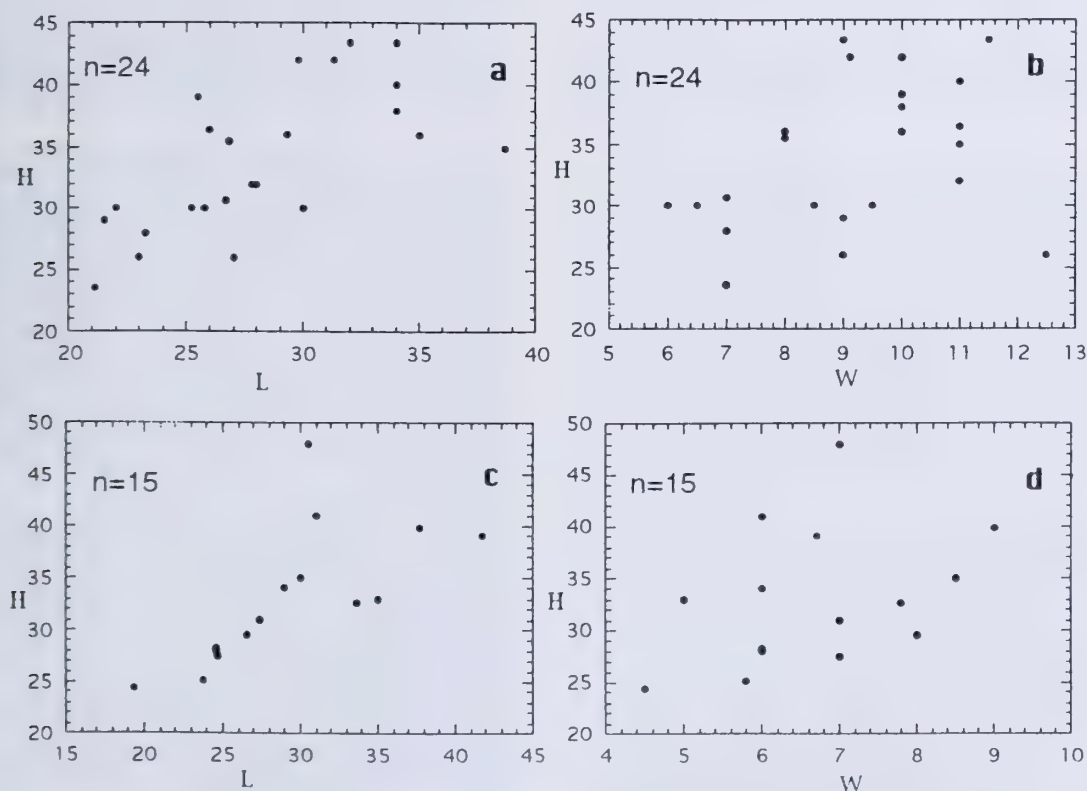


**Figure 2.** Measured characters and some morphologic features of *Cameleolopha* (*Hyotissocameleo*) *tissoti* (Peron and Thomas).





**Figure 3.** Microstructural framework and distribution of diagenetic effects (silicification and dolomitization) in *Cameleolopha* (*Hytissocameleo*) *tissoti* (Peron and Thomas) as seen in radial section.



**Figure 4.** Bivariate scatter diagram of *Cameleolopha* (*H.*) *tissoti* (Peron and Thomas) for height (H) against length (L) and height against width (W). **a, b** for left valves; **c, d** for right valves. *n* = number of valves. H, L and W are in mm.

wall structure. Malchus (1990) proposed a new family Paleolophidae on the basis of the presence of a strongly lenticular, simply foliated microstructure. The carbonate skeleton of "*Ostrea*" *tissoti* in its current state of preservation is entirely made of calcite, as ascertained by Miegen's stain-

ing method. The shell wall is composed of the following layers with different microstructures.

#### Prismatic layer

This is the outermost layer of both valves (Figure 5A). It

**Table 1.** Measurements (in mm) of *Cameleolopha (Hyotissocameleo) tissoti* (Peron and Thomas). Abbreviations: H = Height. L = Length. W = Width (valve concavity). Ah = Height of the adductor muscle pad. Al = Length of the adductor muscle pad. Ad = Maximum diameter of the adductor muscle pad. Dp = No. of dorsal plications (ribs directly connected to the smoothly concentric neanic disc). Pp = No. of peripheral plications (ribs at the shell margin which originated as Dp and extended bifurcationally toward the shell margins). Nos. 1–15 on left and right valves are not of the same individuals.

Specimen number	H	L	W	Ah	Al	Ad	Dp	Pp	Specimen number	H	L	W	Ah	Al	Ad	Dp	Pp
Left valve									Right valve								
1	43.5	32.3	9	8	10	12	9	21	1	33	35	5	-	-	-	8	11
2	39	25.5	10	7	5	9	11	19	2	39	41.8	6.7	-	-	-	9	17
3	36.4	26	11	10	11	12	5	12	3	41	31	6	10	11.7	12.5	7	12
4	28	23.3	7	8	7	9	8	13	4	39.8	37.7	9	11	10	11.5	12	18
5	35.5	26.8	8	10	11	12	10	11	5	35	30	8.5	6.5	10	11	10	14
6	30.7	26	7	9.3	7	9	-	10	6	32.7	33.6	7.8	8	11	11.5	8	12
7	43.5	34	11.5	9.5	11	13	-	14	7	34	29	6	8.5	10	10	7	13
8	40	34	11	14	8	15	6	27	8	28	24.6	6	8.6	8.5	9.2	11	13
9	26	27	12.5	12	7	12	15	18	9	29.6	26.6	8	6	8	10	8	13
10	30	30	6.5	7	8	9	9	14	10	28.3	24.6	6	8	9	10	9	16
11	32	27.8	11	9	12	12	11	15	11	24.4	19.4	4.5	5	6	6.8	8	11
12	30	25.8	9.5	8	6.5	9	12	18	12	25.2	23.8	5.8	4	8	9	8	11
13	35	38.7	11	8	13.3	13.3	5	17	13	31	27.4	7	11	8	11	10	18
14	23.5	21.1	7	7	9	10	10	19	14	48	30.5	7	8.5	11	12	4	8
15	30	22	6	5	9	11	-	12	15	27.5	24.7	7	5	7	8	10	14
16	32	28	11	7.5	10.5	11	-	18									
17	42	31.3	10	11	10	12.5	9	16									
18	38	34	10	-	-	-	10	17									
19	36	35	10	-	-	-	11	14									
20	42	29.8	9.1	-	-	-	10	15									
21	29	21.5	9	8.5	6	10	6	11									
22	36	29.5	8	9	10	11	7	12									
23	26	23	9	6	7	8	6	11									
24	30	25.2	8.5	11	8	11	10	18									

is composed of prisms, about 9  $\mu\text{m}$  long and up to 4.5  $\mu\text{m}$  in diameter. The prisms are arranged slightly oblique to the outer surface of the valve. The prismatic layer has been encountered only in places where the valves are attached to each other and protected from erosion. The preservation of the prismatic layer in this species might be due to burial of the shell in the soft substrate and could not be referred to burial during life as observed in the dorsoventrally elongate oyster *Konbostrea* (Chinzei, 1986).

#### Foliated layers

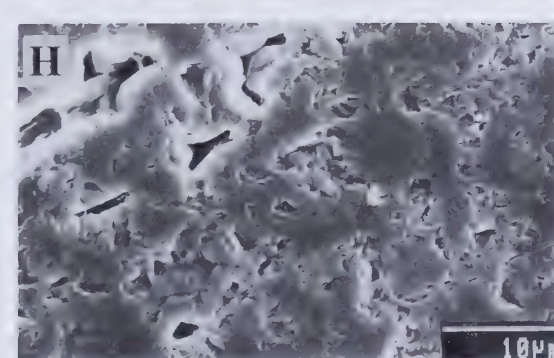
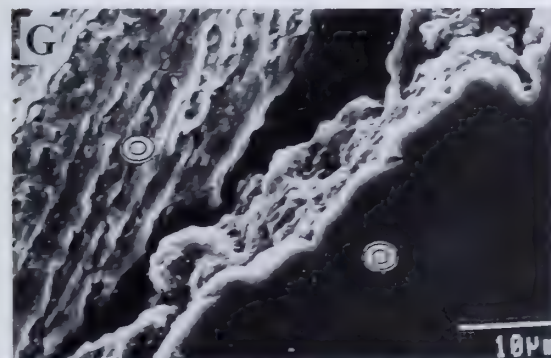
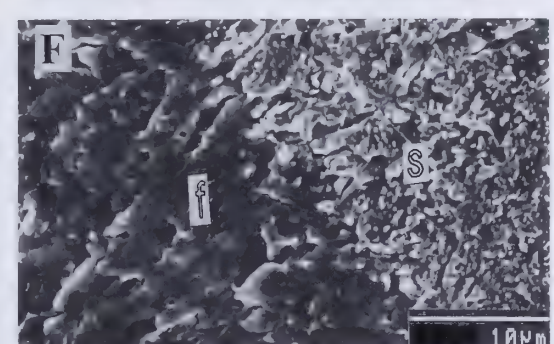
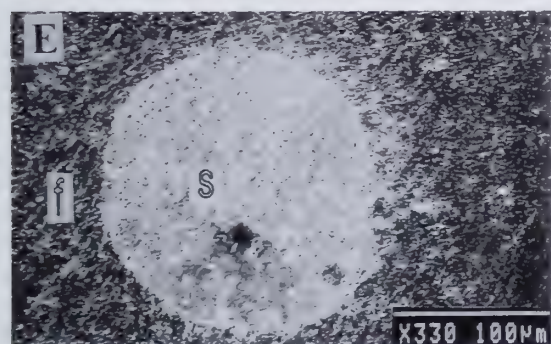
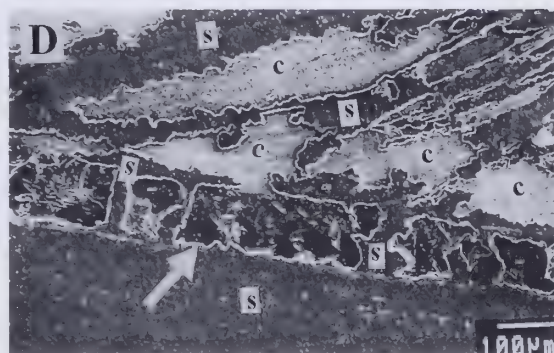
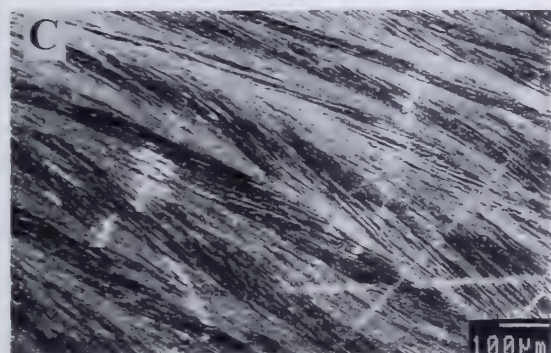
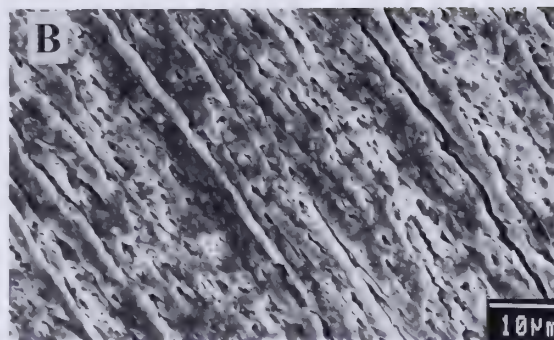
There are two types of foliated structures. One is the

regular type and the other is the crossed-foliated structure, in which the foliated sheets cross each other at a low angle.

**Regularly foliated structure.**—This structure is synonymous with the simply foliated structure of Malchus (1990). It is built up of long, thin calcitic laths with pointed ends, arranged parallel to one another to form a foliated sheet. The sheets are, in turn, arranged nearly parallel to one another. The orientation of sheets parallels the general trend of shell architecture (Figure 3). The shell architecture is influenced by shell morphology. The regularly foliated structure is predominant in this species, as it constitutes the structural framework of the shell, between the outer prismatic layer

→ **Figure 5.** Microstructure of *Cameleolopha (Hyotissocameleo) tissoti* (Peron and Thomas). **A.** The outer prismatic layer (arrow) of the lower individual (a) below the dark groove (cementing zone of the upper oyster), radial section. **B.** Regularly foliated sheets in the umbonal area, radial section. **C.** Herringbone cross-foliated structure, radial section. **D.** Differential response of the calcitic structure (low relief, shown as c) and the more resistant secondary silica (high relief, shown as s) to the etching acid; the adductor myostracum is indicated by arrow. **E.** Spherical unit (s), as a secondary product of recrystallization, with its smooth rounded boundary embedded in a foliated layer (f), parallel section. **F.** Higher magnification of **E**, showing the fine homogeneous filling of the spheres. **G.** Silicified sheets (lower right) normal to the adjacent unit of foliated sheets (upper left) with corroded contact, the circled spots indicate the locations of the microprobe investigations, transverse section. **H.** Silicified foliated structure with cavities of various shapes, radial section.







and the innermost regularly foliated layer (Figures 3 and 5B).

**Herringbone cross-foliated structure.**—At low magnification we observed some layers, each consisting of two sublayers, in the middle part of the shell cross-section (Figure 3). The second-order elements of each sublayer are parallel to one another, inclined at an acute angle to the opposite sublayer. As a result, the sublayers show a regular alternating pattern (Figure 5C). This arrangement of foliated sheets was called "herringbone cross-foliated structure" by Malchus (1990).

#### Adductor myostracum

The relict of adductor myostracum, ranging from 0.3 to 0.35 mm in thickness, is easily traceable in the specimens examined although it does not retain its original, probably aragonitic, microstructure (Figure 5D). It is composed of coarse-grained calcite. The calcite layer filling the space of the myostracum was fractured and partly replaced by silica mineral (Figures 3 and 5D). Preservation of relicts of original aragonitic crystallites have been reported, even in Paleozoic fossils (Rollins, 1966; Carter and Tevesz, 1978). In these cases, the aragonite is often preserved within the silicified part of the shell, but we could not find aragonite in this Cretaceous oyster. This suggests that silicification occurred after alteration of the myostracal aragonite to stable calcite.

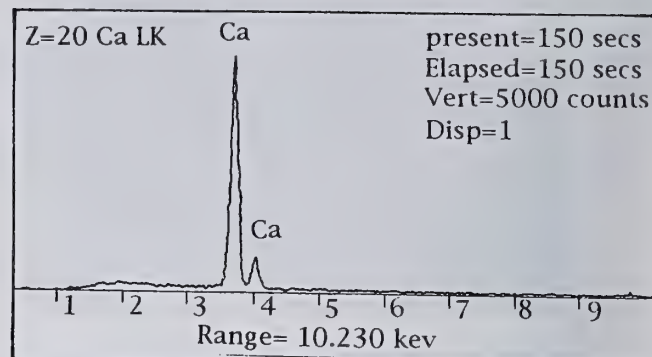
The microstructure of this species does not show any sign of chalky deposits or chambers within its shell. The absence of chalky deposits in oyster of the Lophinae was mentioned by Torigoe (1981) as one of the characteristic differences between them and members of the Ostreinae, besides the obvious chomata and other characters of the soft parts. Chinzei and Seilacher (1993) reported accidental chambering in the shell of a Recent *Lopha*, the chambers being filled with dendritic calcite crystals characterized as a "Christmas tree". Aqrabawi (1993) has broadened the characteristic morphological range of *Nicaisolopha* Vyalov, 1936, to include the presence of some empty and chalky lenses within its simply foliated structure. So, the absence of empty lenses and chalky deposits in the species examined here is worth noting. This supports its affinity to the Lophinae as well as its exclusion from genus *Nicaisolopha*.

#### Diagenetic alteration in shell microstructure

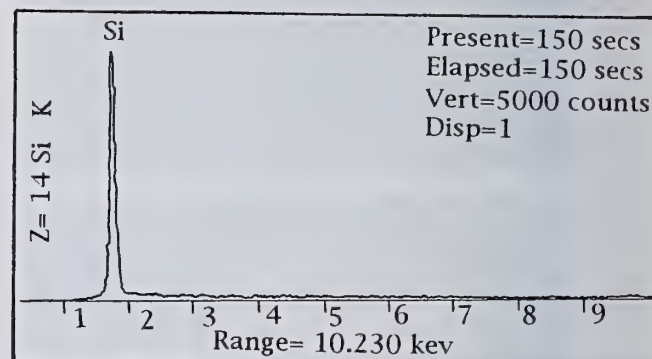
Diagenetic alterations in the shell microstructure are expressed by silicified foliated structure and recrystallized spheroidal units.

**Silicified foliated structure.**—A quasihomogeneous structure occupies the inner part of the shell near the umbo. This area tapers toward the anterior, posterior and ventral margins (Figure 3). We can observe the original sheets of foliated structure only in some well-prepared sections (Figure 5H). The homogeneous material is made up of large crystals of a silica mineral detected by microprobe analysis (Figure 6) and SEM observations (Figures 5G, H). The silicification is seen mainly in the inner part of the shell. This is consistent with the view that silicification tends to start in the internal parts of the shell and spread outward (Suzuki *et al.*, 1993). Suzuki *et al.* (1993) observed that

#### Foliated part



#### Altered part



**Figure 6.** Microprobe chart for a spot of foliated structure, showing a predominance of **Ca** (above) and the altered part showing predominance of **Si** (below).

silicification has been recorded in such bivalves with originally aragonitic shells as glycymerids and venerids, and that it plays a significant role in preserving the original aragonitic structures. This study reveals that silicification can also occur in originally calcitic shells, leading to disordering of the original fabrics of shell microstructure.

**Spheroidal units.**—Many spheroidal units, each 150 to 200  $\mu\text{m}$  diameter (Figure 5E), are observed as sporadic spheres in the mid-ventral part of the shell. These spheres are composed of fine (1.1 to 5.5  $\mu\text{m}$ ) aggregates of calcite that are irregularly shaped and have no preferred orientation. These aggregates have the appearance of a homogeneous structure (Figure 5F). Figure 5F also shows the sudden change in lath size and arrangement of the calcitic aggregates of this spherical units and its surrounding foliated structure. This arrangement with its false homogeneous appearance is considered to be a secondary product of recrystallization processes.

#### Systematic description (by M. Zakhera)



Family Ostreidae Rafinesque, 1815  
Subfamily Lophinae Vyalov, 1936

**Discussion.**—As the species seems to be a lophine oyster, relevant systematic views are briefly reviewed.

Vyalov (1936) established the subfamily Lophinae in the family Ostreidae for the oysters having radially sculptured valves and a plicated or undulating commissure. At the same time, he described the sculpture of *Nicaisolopha* as vague folds. According to Stenzel (1971), the subfamily Lophinae includes the genus *Lopha* Röding, 1798 with subgenera *Abruptolopha* Vyalov, 1936 and *Actinostreon* Bayle, 1878; the genera *Alectryonella* Sacco, 1897, *Cameleolopha* Vyalov, 1936, *Nicaisolopha* Vyalov, 1936 and *Rastellum* Faujas de Saint-Fond, 1799, with subgenus *Arctostrea* Pe rinquière, 1910. Recently, *Arctostrea* has been treated as a discrete genus (Carter, 1968; Zakhera and Kassab, 1999). In light of Thomson's (1954) work, Stenzel (1971) considered *Alectryonia* Fischer de Waldheim, 1808, *Dendostrea* Swainson, 1835 and *Pretostrea* Iredale, 1939, as synonymous of *Lopha* Röding. Meanwhile Torigoe (1981) morphologically discriminated *Dendostrea* Swainson, 1835 as a separate genus not equivalent to *Lopha*. Malchus (1990) emphasized the importance of shell microstructure rather than shell morphology in his classification of Mesozoic oysters. Consequently, he referred the Cretaceous *Nicaisolopha*, which has a typical lophine form and was formerly assigned to the Lophinae, to his new ostreid subfamily Liostreinae Malchus, 1990. At the same time he erected, on the basis of a characteristic microstructure, another new family, Palaeolophidae, for some other Mesozoic lophine oysters, including *Rastellum* Faujas de Saint-Fond, 1799, *Palaeolopha* Malchus, 1990, and *Oscillophya* Malchus, 1990. He also pointed out that *Cameleolopha* Vyalov, 1936 could be synonymous with *Nicaisolopha* Vyalov, 1936.

A large sample of the present species, in a very good state of preservation, enables us to examine its morphological and microstructural characters precisely, to take the effects of homeomorphy into account and determine its proper systematic position. The species has recently been placed in the genus *Nicaisolopha* Vyalov, 1936. According to Stenzel (1971), *Nicaisolopha* Vyalov, 1936 is mainly characterized by 4–7 radial folds that are not dichotomous; the folds are undulatory, round-crested, and separated by equal, rounded interspaces, on both valves. The genus has no chomata; the adductor muscle imprint is reniform, deeply concave at its dorsal margin; the ligamental area is low and long; the left valve resilifer is shallowly excavated and slightly longer than the bourrelets; and the right valve resilifer is flat, with growth squamae slightly raised in the later growth stage.

On the other hand, "*Ostrea*" *tissoti* Peron and Thomas has 10–27 clearly dichotomous (sometimes trichotomous) radial ribs, rather than broad radial folds as in *Nicaisolopha*. This species is smaller in size and it has distinct chomata, which are absent in *Nicaisolopha* and *Cameleolopha* s.s. It has a reniform to comma-shaped adductor muscle imprint and a resilifer deeply excavated in the left valve that is about two times longer than the bourrelets. Compact, closely spaced growth lines, rather than growth squamae, tend to be promi-

nent at the end of growth phases. Based on these characteristics, I transferred this species from *Nicaisolopha* to *Cameleolopha*.

Genus *Cameleolopha* Vyalov, 1936

**Type species.**—*Ostrea cameleo* Coquand, 1869.

Subgenus *Hytissocameleo* Zakhera subgen. nov.

**Derivation of name.**—From a combination of *Hytisso*, in reference to its general hyotissine form and *Cameleo*, in reference to the genus name *Cameleolopha* Vyalov, 1936.

**Type species.**—*Ostrea tissoti* Peron and Thomas, 1891.

**Diagnosis.**—Shell having numerous fine chomata and relict chomata. Resilifer long. Radial ribs narrow with rounded crests tending to start from the umbonal area, and branching dichotomously or trichotomously.

**Comparison.**—*Hytissa* Stenzel, 1971 has only a superficial resemblance to *Hytissocameleo* in its general shell form. They differ in shell microstructure, shape of adductor scar and the style of ornamentation. *Hytissocameleo* differs from *Cameleolopha* s. s. in the following points:

1. Possession of distinct chomata and relict chomata (not mentioned in the designation of *Cameleolopha* s.s. in Stenzel, 1971, probably they were very weak and overlooked).

2. Existence of wider range in the number of radial ribs (10 to 27 as peripheral ones), while the number ranges from 12 to 20 in *Cameleolopha* s.s.

3. In *Hytissocameleo*, the radial ribs are straight or weakly undulating in their crest direction, continuous from near the umbo to the commissure as a general trend, and dichotomously or trichotomously branching. In *Cameleolopha* s.s. the radial ribs are, by contrast, curved and diverge outward as the animal grows.

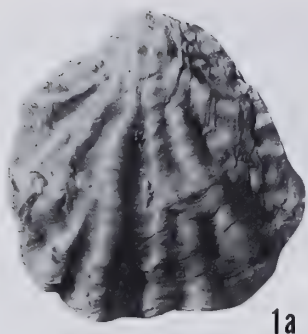
4. The radial ribs in *Hytissocameleo* have rounded crests, while these are angular in *Cameleolopha* s.s.

The Cenomanian species *Ostrea cameleo* Coquand, 1869, the type species of the genus *Cameleolopha*, can be distinguished from *Ostrea tissoti* Peron and Thomas by the characters noted above. The material identified as *Hytissa armata* (Goldfuss) by Pugaczewska (1977, p.194, pl. 12, figs. 4–5) from Poland, has bifurcated radial ribs, compact and closely spaced growth lines and a high ligamental area with deep resilifer. So it might be included in *Hytissocameleo*. *Cameleolopha bellaplicata* (Conrad) could be attributed to the subgenus *Hytissocameleo* as it has the same shell form and style of ornamentation.

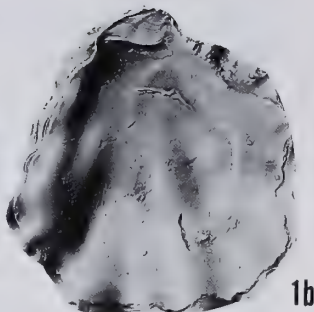
*Cameleolopha pauciplicata* Kassab and Mohamed, 1996 has weak chomata and differs from *Cameleolopha* (*Hytissocameleo*) *tissoti* in having a triangular shell form that is tapering dorsally, has fewer number of angular, curved dichotomous radials and no relict chomata.

On the basis of the presence of weak chomata in some species of *Cameleolopha* s.s., the shape and position of the adductor muscle and the ribbing ornamentation, *Cameleolopha* s.s. and *Hytissocameleo* came from the same ancestor, which was probably "*Ostrea*" *loriolis* Coquand and/or "*Ostrea*" *cornuelis* Coquand in the

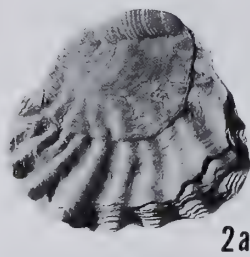




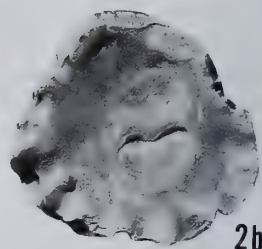
1a



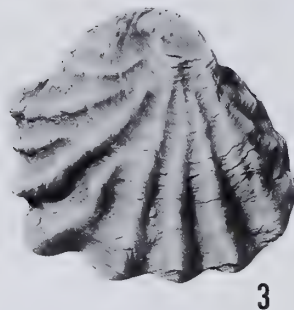
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2a



2b



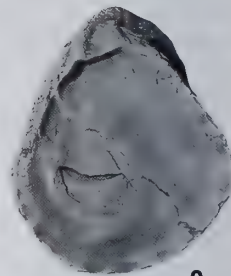
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4



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6



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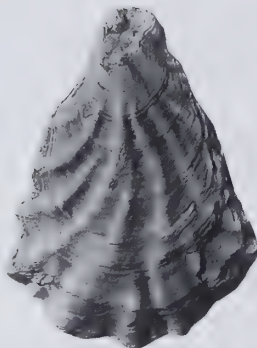
8a



8b



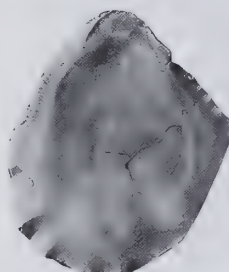
8c



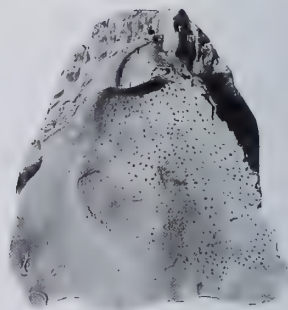
9a



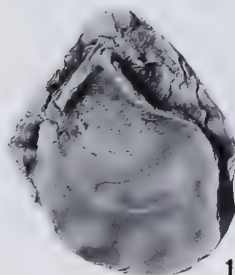
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10



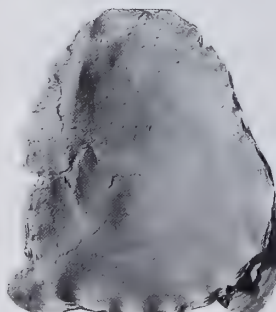
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12



13



14



15



Neocomian passing by "*Ostrea*" *complicata* Mahmoud in the Albian and *Lopha syphax* Coquand in the Cenomanian.

***Cameleolopha (Hyotissocameleo) tissoti***  
(Peron and Thomas, 1891)

Figure 7

*Ostrea forgemolli* Coquand, 1869, p. 25, pl. 2, figs. 9–11 (non figs. 1–8).

*Ostrea tissoti* Peron and Thomas, 1891, p. 196, pl. 24, figs. 1–7.

*Alectryonia tissoti* (Peron and Thomas). Daqué, 1903, p. 365, pl. 34, figs. 11–12.

*Lopha tissoti* (Peron and Thomas). Fourtau, 1917, p. 54, pl. 5, figs. 1–5; Bandel *et al.*, 1987, pl. 2, figs. 5a, b.

*Nicaiolopha tissoti* (Peron and Thomas). Kuss and Malchus, 1989, p. 902; Malchus, 1990, p. 174, pl. 19, figs. 7–16, 18.

**Material.**—One hundred and twenty-seven specimens, as separated left and right valves, conjoined valves and a few fragments, have been collected from yellowish-brown, marly mudstone of Campanian sediments (Duwi Formation) in Wadi Tarfa of the northern part of Eastern Desert of Egypt. They are housed in the Geological Museum of Aswan University, bearing the prefix KZASW with serial numbers.

**Measurements.**—Measurements on complete specimens are listed in Table 1.

**Description.**—Shell small in size (up to 5 cm), not strongly inflated, subequivalve. Outline suborbicular to spatulate. No auricles. Left valve (LV) more capacious than right valve (RV). Maximum convexity of valve occurs ventrally, corresponding to position of adductor muscle. Umbo terminal, pointed. No umbonal cavities in most individuals while some left valves have a small and very shallow one beneath hinge plate. Chomata well developed both anterodorsally and posterodorsally in vicinity of hinge. Anachomata on right valve long (up to 2 mm), thin, closely arranged, straight and sometimes tilted in same valve. Corresponding catachomata on left valves less pronounced and easily overlooked in some valves. Relict chomata also present. Ligament triangular, high in left valve, low in right valve; straight or posteriorly or anteriorly curved. Ligament area tripartite with a resilifer twice as broad as both bourrelets, or slightly more. Anterior bourrelet longer than posterior one. Adductor muscle imprint comma-shaped in elongated individuals, kidney like in suborbicular ones, and situated posteroventrally. Quenstedt muscle insertions very small, located below resilifer. Attachment area small to medium on left valves with corresponding xenomorphic areas on right valves. Medium-sized attachment area might distort

shell shape and sculpture. Neanic part of shell smooth. Both valves have narrow round-crested radial ribs, always at least dichotomous, sometimes trichotomous, especially on shell periphery. They are usually 10–18 in number and may attain 27 in number along shell margin. These radials are crossed by tight nonappressed growth lamellae which are intermittently prominent. Commissure plicate, interlocking at valve margin. Plication impressed on internal valve surface only for thin-shelled valves.

**Occurrence.**—It seems likely that *Cameleolopha (Hyotissocameleo) tissoti* (Peron and Thomas) is a well represented Tethyan species in North Africa. The species was recorded from the same age interval from Tunisia by Peron and Thomas, 1891. It was also recorded from Tripoli by Krumbeck (1906) under the name of *Ostrea* *cfr. forgemolli* Coquand.

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◀ **Figure 7.** *Cameleolopha (Hyotissocameleo) tissoti* (Peron and Thomas). All figures in natural size. **1a, b.** KZASW 4/7–1. External and internal views of a typical rounded right valve, showing bifurcating radial ribs, dorsal catachomata and comma-shaped adductor pad. **2.** KZASW 4/7–2. **2a.** External view of a right valve showing xenomorphic area and prominent lamellae marking the growth phases. **2b.** Internal view of **2a**. **3–5.** External views of left valves showing different shapes and sizes of the attachment area. **3.** KZASW 4/7–3. **4.** KZASW 4/7–4. **5.** KZASW 4/7–5. **6.** KZASW 4/9–1. Internal view of a right valve. **7, 11.** KZASW 4/11–1. Two cemented left valves. **8a, b.** KZASW 4/7–6. External views of right valves, showing "zigzag" commissure. **9a, b.** KZASW 4/7–7. External and internal views of a typical spatulate left valve, showing radial bifurcating, and deep, wide resilifer. **10.** KZASW 4/9–2. Internal view of a right valve. **12.** KZASW 4/7–8. Cemented right valve with another left valve. **13.** KZASW 4/11–2. Internal view of a right valve. **14.** KZASW 4/11–3. Internal view of a right valve, showing a different outline and different resilifer size and orientation. **15.** KZASW 4/7–9. Left valve with fewer radial ribs but still ventrally bifurcated.



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# Molecular phylogeny and morphological evolution of laqueoid brachiopods

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**Abstract.** One of the virtues of molecular phylogeny for paleontology is that it can provide independent and often reliable sets of data from living relatives to test various evolutionary hypotheses inferred from fossil forms. In this study, we present results of a molecular phylogenetic analysis of 12 species of 7 genera belonging to the Laqueoidea, which is the most prolific of the brachiopod superfamilies in the seas around Japan. Onto a phylogenetic tree based on partial sequences (1218 bp) of the mitochondrial *cox1* gene, we superimposed various external and internal morphologic characters of both juveniles and adults for the taxa examined. The resulting patterns indicated that several lineages experienced paedomorphic evolution in terms of the brachidial (loop) morphology, and that, contrary to some traditional views, certain adult features, such as the bilateral loop, possession of a cardinal process, and a rectimarginate commissure, had homoplasious distributions. Examination of the character distributions also revealed, however, that anterior nonbifurcation of the septal pillar at the axial phase is a synapomorphy for a major clade recognized in the molecular analysis. Those results suggest that early loop ontogeny, information about which is still fragmentary, would be useful in assessing relationships among laqueoid brachiopods, including certain Mesozoic genera.

**Key words:** Brachiopoda, cytochrome c oxidase I (*cox1*) gene, Laqueoidea, loop ontogeny, mitochondrial DNA, molecular phylogeny, Recent

## Introduction

The Laqueoidea is one of the larger terebratulide brachiopod superfamilies, being well represented in both present-day waters and Cenozoic strata of Japan. The members of this superfamily, as well as other superfamilies within the order Terebratulida, are characterized by the possession of calcareous internal skeleton known as the loop which continually undergoes considerable morphological change during growth before attaining the full adult stage. Due to its complexity and diversity, loop morphology has been the prime tool for the inference of phylogenetic relationships among laqueoid brachiopods and for the classification of long-looped brachiopods generally at various taxonomic levels (Hatai, 1936, 1940; Muir-Wood *et al.*, 1965; MacKinnon, 1993). However, the assumption that loop morphology reflects phylogeny has not been fully tested, nor has it been possible to discuss loop evolution without the risk of circular arguments. Ideally phylogenies should be based on characters that are completely independent of the loop. One such would be molecular characteristics.

Although molecular trees are only working hypotheses of the true evolutionary relationships of living species, they are useful in providing a basis for discussion of the likely history of a character of interest. In studies of morphological character states, predictions can be made about the probable direction of morphological character state transformations and combinations of characters in basal versus derived species, and therefore we can reassess the morphological characters that support the relationships. Because only morphological characters can be used to establish the phylogenetic affinities of ancient fossil taxa, the success of a morphological approach for fossils can be increased greatly if patterns of character state evolution are considered in the light of an independently estimated phylogeny.

Previous brachiopod molecular systematics have been based on immunological comparisons of shell macromolecules (Collins *et al.*, 1988; Curry *et al.*, 1991; Endo *et al.*, 1994) and on nucleotide sequence comparisons of nuclear 18S ribosomal ribonucleic acids (rRNA) and mitochondrial 12S rRNA (Cohen and Gawthrop, 1996, 1997; Cohen *et al.*, 1998a, 1998b). The novel overall patterns of loop evolution

that the immunological data indicated were largely unsupported by the results of 18S rRNA sequence comparisons (Cohen and Gawthrop, 1997; Cohen *et al.*, 1998b). Besides, it was difficult using the immunological data to resolve relationships among closely related genera. Even with the 18S rRNA data, which offered direct measurements of molecular similarity and thus are more reliable, detailed relationships among the long-looped terebratulide brachiopods remained unclear because the tempo of the 18S rRNA sequence evolution was considered too slow to provide adequate variations among these forms (Cohen *et al.*, 1997).

Both the nucleotide and amino acid sequences of the mitochondrial cytochrome c oxidase subunit I (*cox1*) gene turned out to provide a potentially useful framework for shallower phylogenies, especially of the relationships among the long-looped laqueoid brachiopods (Saito *et al.*, 2000). In this paper, we report the phylogenetic relationships of laqueoid brachiopods inferred from the *cox1* sequences and discuss evolutionary processes of the loop and of other morphologic characters in laqueoid brachiopods, including some possibly basal Mesozoic fossils.

### Material and methods

**Brachiopod samples and molecular phylogenetic analysis.**—Twenty-seven specimens representing a total of 16 species of terebratulide brachiopods including 11 laqueoid species were available for this study (Table 1).

Full details of DNA extraction, amplification and sequencing methods are described in Saito *et al.* (2000). In brief, *cox1* sequences (1218 bp or 406 amino acids in length) were obtained by the direct sequencing of DNA amplification products synthesized by PCR. Amino acid sequences were deduced by reference to the genetic code of brachiopod mitochondrial DNA (Saito *et al.*, 2000). Phylogenetic analysis by maximum-parsimony (MP) was performed with PAUP version 3.1 (Swofford, 1993), using the exhaustive search algorithm and equal weighting for all substitutions. To evaluate the robustness of the internal branches, 500 bootstrap replications were executed. Analysis by neighbor-joining (NJ; Saitou and Nei, 1997) and maximum-likelihood (ML) were performed with Molphy version 2.3 (Adachi and Hasegawa, 1996a) using the mtREV24-F model (Adachi and Hasegawa, 1996b) for amino acid data and HKY85 model for nucleotide data (Hasegawa *et al.*, 1985), using the "Local Rearrangement Search" option. For each internal branch, a local bootstrap probability (LBP) was estimated by the RELL method (Kishino *et al.*, 1990) with 1000 replications. TreeView version 1.4 (Page, 1996) was used to draw trees.

Because of the low intraspecific nucleotide sequence variations in the examined individuals (less than 2%), and the lack of any amino acid difference within each species, one individual was selected to represent the species in the phylogenetic analysis. These representative nucleotide sequences will appear in the DDBJ nucleotide sequence database with the Accession Numbers AB026501–AB026516 shown in Table 1.

For analysis of deeper relationships within the Laqueoidea, both the amino acid and the 1st and 2nd codon

**Table 1.** Specimens used in this study and their sampling localities. Accession numbers refer to the DDBJ nucleotide sequence database.

Species	Locality	Accession number
<b>Ingroup</b>		
(Laqueoidea)		
<i>Laqueus rubellus</i> 1	Sagami Bay	AB026501
<i>L. rubellus</i> 2	Sagami Bay	
<i>L. rubellus</i> 3	Sagami Bay	
<i>L. blanfordi</i>	Otsuchi, Tohoku	AB026502
<i>L. quadratus</i> 1	SW of Oshima	AB026505
<i>L. quadratus</i> 2	SW of Oshima	
<i>L. californicus</i>	Monterey Bay, California, USA	AB026503
<i>L. c. vancouveriensis</i>	Monterey Bay, California, USA	AB026504
<i>Pictothyris picta</i> 1	off Mishima	AB026506
<i>Pictothyris picta</i> 2	Sagami Bay	
<i>Jolonica nipponica</i>	Izu Islands, W of Takase	AB026509
<i>Frenulina sanguinolenta</i> 1	Vava'u, Tonga	AB026510
<i>F. sanguinolenta</i> 2	Vava'u, Tonga	
<i>Shimodaia pterygiota</i> 1	Off Shimoda	AB026511
<i>S. pterygiota</i> 2	Off Shimoda	
<i>Terebratalia coreanica</i> 1	Otsuchi, Tohoku	AB026508
<i>T. coreanica</i> 2	Wakkanai, Hokkaido	
<i>Coptothyris grayi</i> 1	Otsuchi, Tohoku	AB026507
<i>C. grayi</i> 2	Wakkanai, Hokkaido	
<b>Outgroup</b>		
(long-looped forms)		
<i>Ecnomiosa</i> sp. 1	Izu Islands	AB026512
<i>Ecnomiosa</i> sp. 2	Izu Islands	
<i>Campages</i> sp.	SW of Yonejima	AB026513
<b>Outgroup</b>		
(short-looped forms)		
<i>Terebratulina crosseii</i>	Otsuchi, Tohoku	AB026514
<i>Terebratulina pacifica</i>	off Oshima	AB026515
<i>Gryphus davidsoni</i>	S of Oshima	AB026516

position nucleotide sequences were used as data sets. Because little variation was detected in the amino acid sequences and the 1st and 2nd codon positions of nucleotide sequences, analyses of five *Laqueus* species were performed separately with full lengths of the nucleotide data.

**Morphological observations.**—Observation of juvenile loop morphologies of two laqueoid species, *Jolonica nipponica* and *Terebratalia coreanica*, was carried out on a Hitachi S-2400S Scanning Electron Microscope using the methods described by Saito (1996).



## Results

### Laqueoid relationships

Of the terebratulides analyzed, *Ecnomiosa* sp. and *Campages* sp. clustered basal to the laqueoids and monophyly of laqueoids were strongly supported (100% LBP, Figure 1). Therefore, we used *Ecnomiosa* sp. and *Campages* sp. as the outgroups for the analyses of all laqueoids sampled and within the species of *Laqueus*. Analyses were also made for an ingroup comprising the 6 genera of Laqueoidea using *Laqueus rubellus* as outgroup.

Analyses based on different tree-building methods (NJ, ML, and MP) and different data sets converged to indicate four possible topologies for the relationships among laqueoid genera (Trees 1 to 4; Figure 2). The results of the molecular phylogenetic analysis are summarized in Figure 3.

All resulting trees clearly indicated the basal placement of *Laqueus* in the Laqueoidea. The local bootstrap support of this node is high in all analysis (99–100%). Among the remaining six genera (*Terebratalia*, *Coptothyris*, *Shimodaia*, *Frenulina*, *Pictothyris* and *Jolonica*), the close relationship between *Jolonica* and *Pictothyris* is consistently supported by high bootstrap values (82–99%). Three of the four trees (Trees 1 to 3) show very similar topologies: the close association of *Shimodaia*-*Frenulina*-*Pictothyris*-*Jolonica*, with *Terebratalia* and *Coptothyris* left outside. The positions of *Terebratalia* and *Coptothyris* differ slightly in each tree but

they are generally positioned close to one another in the four cladograms. Tree 4 shows early branching of *Shimodaia* within the 6 genera.

The NJ analysis consistently supported Tree 1 (Figure 2). The ML analysis supported Tree 1 or Tree 2, however, the log-likelihood differences among Trees 1 to 3 are very small when amino acid sequences are used. The LBP support for the branch including *Terebratalia* or *Coptothyris* is low (19–

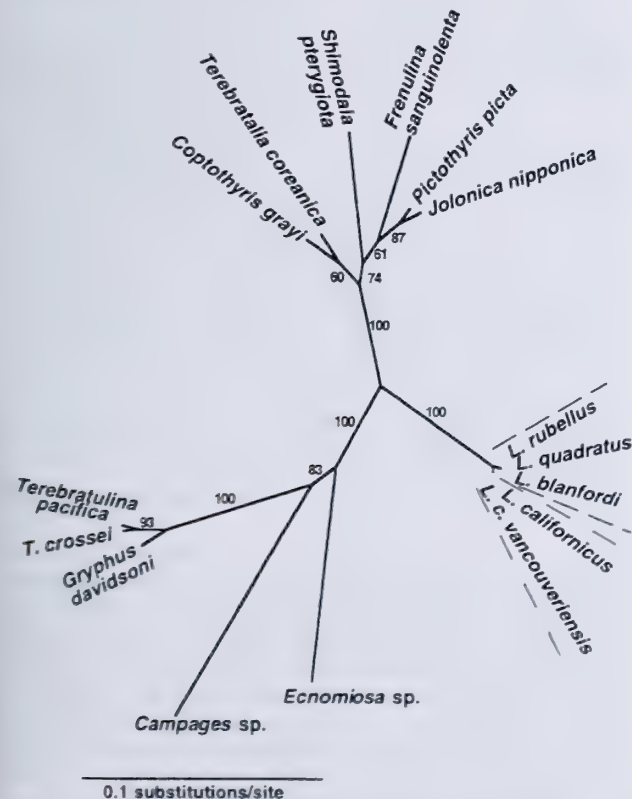
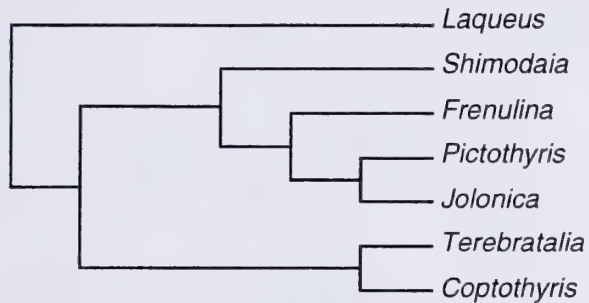
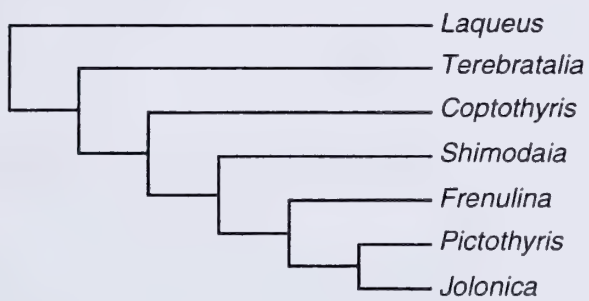


Figure 1. NJ tree based on amino acid sequences. The number at each internal node of the tree indicates the percentage of node occurrence in 500 bootstrap replicates.

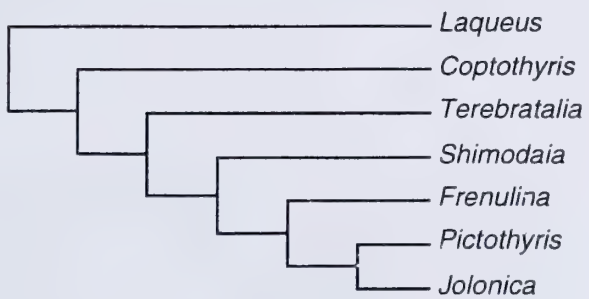
Tree 1



Tree 2



Tree 3



Tree 4

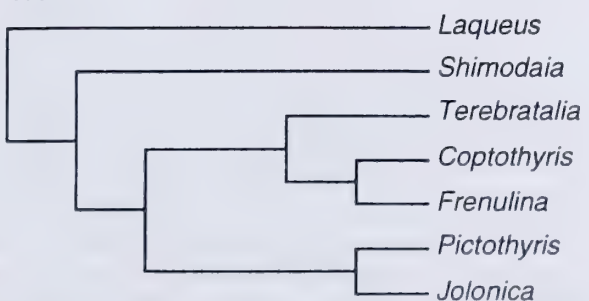


Figure 2. Four possible topologies for the relationships among laqueoid genera.

Tree ID.	Tree topology	MP		ML			
				aa		1st+2nd	
		aa	1st+2nd	InL	BP	InL	BP
Tree 1	((Laq,(((Pic,Jol),Fre),Shi),(Tra,Cop))),Ecn,Cam)	228	349	-2418.64±109.10(ML)	0.2887	-2855.96±101.53(ML)	0.4484
Tree 2	((Laq,(((Pic,Jol),Fre),Shi),Cop),Tra)),Ecn,Cam)	230	351	-2419.42±108.87(-0.8)	0.2626	-2863.78±102.18(-7.8)	0.0369
Tree 3	((Laq,(((Pic,Jol),Fre),Shi),Tra),Cop)),Ecn,Cam)	228	349	-2419.54±109.61(-0.9)	0.2410	-2859.35±101.83(-3.4)	0.2996
Tree 4	((Laq,(((Pic,Jol),Fre),(Tra,Cop)),Shi)),Ecn,Cam)	226(MP)	348(MP)	-2423.61±109.48(-5.0)	0.2077	-2860.59±101.85(-4.6)	0.2151

Tree ID.	Tree topology	MP		ML			
				aa		1st+2nd	
		aa	1st+2nd	InL	BP	InL	BP
Tree 1	(Laq,(((Pic,Jol),Fre),Shi),(Tra,Cop)))	125	206	-1852.65±77.85(-5.5)	0.0715	-2183.02±75.88(-3.9)	0.0891
Tree 2	(Laq,(((Pic,Jol),Fre),Shi),Cop),Tra))	124	206	-1847.14±77.19(ML)	0.6903	-2179.14±75.71(ML)	0.4130
Tree 3	(Laq,(((Pic,Jol),Fre),Shi),Tra),Cop))	124	206	-1852.30±78.06(-5.2)	0.1245	-2182.64±75.92(-3.5)	0.1915
Tree 4	(Laq,(((Pic,Jol),Fre),(Tra,Cop)),Shi))	123(MP)	205(MP)	-1861.79±79.67(-14.6)	0.1137	-2182.97±76.15(-3.8)	0.3064

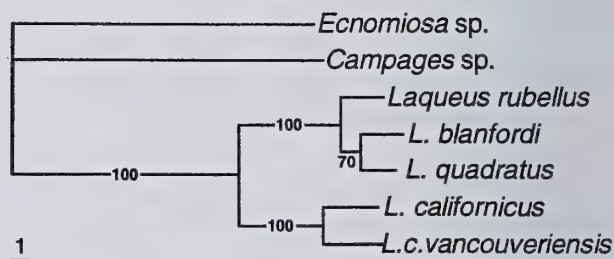
**Figure 3.** Summary of phylogenetic analysis showing the total maximum parsimony tree length, the log-likelihood ( $\pm$  standard errors) and the bootstrap probabilities for each of the plausible trees. Species name abbreviations: Laq = *Laqueus rubellus*, Pic = *Picthothyrus picta*, Jol = *Jolonica nipponica*, Fre = *Frenulina sanguinolenta*, Shi = *Shimodaia pterygiota*, Tra = *Terebratalia coreanica*, Cop = *Coptothyris grayi*, Ecn = *Ecnomiosa* sp., Cam = *Campages* sp. Upper Box: relationships of 7 laqueoid genera with *Ecnomiosa* sp. and *Campages* sp. as outgroup. Lower Box: relationships of 6 laqueoid genera (*Shimodaia*, *Frenulina*, *Jolonica*, *Picthothyrus*, *Coptothyris*, *Terebratalia*) with *Laqueus rubellus* as outgroup. aa: amino acid data. 1st + 2nd: nucleotide data of 1st and 2nd codon positions.

66%) in all analyses. The node of the *Shimodaia-Frenulina-Picthothyrus-Jolonica* clade is supported by moderate to high LBPs (70–100%).

The MP analysis consistently supported Tree 4 (Figure 2). However, the tree length differences amongst the four trees are only one or two steps (Figure 3). Besides, the Retention Index (RI) for all four topologies was also relatively low (RI = 0.446–0.663), indicating that support for Tree 4 in MP analysis is not strong. When 500 bootstrap replicates were performed, the resulting consensus trees showed either unresolved trichotomy or the clustering of *Shimodaia-Frenulina-Picthothyrus-Jolonica* with a low BP value (51–56%). It is known that the MP analysis is more susceptible to 'unequal rate effects' than the NJ or ML analysis, and can lead to a wrong tree when the nucleotide substitution rates greatly vary among different branches (Saitou and Imanishi, 1989). The observed branch length variation among the ingroup taxa (Figure 1) suggests that the tree indicated by the MP analysis may not be reliable.

These results lead to the conclusion that any one of Tree 1, 2, or 3 represents the best estimate of the true phylogeny, but the available *cox1* data being inadequate to make a final determination from among them. More data are needed to resolve the positions of *Terebratalia* and *Coptothyris*. Thus, the strict consensus tree of Trees 1 to 3 is proposed as a basis for reconstruction of laqueoid evolution.

Figure 4 gives the ML tree of 5 species of the genus *Laqueus*. Two coherent groups were assessed; (1) the Japanese group (*L. rubellus*, *L. blanfordi*, *L. quadratus*) and (2) the North American group (*L. californicus*, *L. c. vancouveriensis*). Each cluster was supported by a high LBP value (100%). The NJ and MP analyses yielded the



**Figure 4.** NJ tree of *cox1* nucleotide sequences for the relationships within the genus *Laqueus*. The same topology was obtained by other methods of analysis (MP and ML). The numbers in the tree represent LBP values.

same tree topology.

#### Character state distributions among laqueoid brachiopods

Molecular analyses of *cox1* sequences, as described above, provide a preliminary framework for the elucidation of phylogenetic relationships among some laqueoid brachiopods. Onto this molecular framework, we superimposed some morphological characters of those brachiopods, such as shell traits (outline, commissure shape and coloration), adult loop morphology, cardinalia at the annular phase of loop ontogeny, and type of the septal pillar at the axial phase (Figure 5). Details of the selected morphological characters for each species are summarized in Table 2. Loop ontogenetic series of laqueoid species are shown in Figure 6. Figure 7 illustrates hitherto undescribed early loop stages of *Terebratalia coreanica* and *Jolonica nipponica*.



**Table 2.** Comparisons of selected morphological characters of 7 species of the Laqueoidea.

Species	maximum size (cm)	adult loop pattern	axial/annular septal pillar	cardinalia	cardinal process	deltidial plates in adult	ornament and coloration
<i>Laqueus rubellus</i>	3.5	bilateral	bifurcate	inner and outer hinge plates, inner resting on the median septum	absent	conjunct	yellowish red with stripes
<i>Pictothyris picta</i>	3.5	latero-vertical	nonbifurcate	no inner hinge plates, the cardinalia are divergent	present	conjunct	irregular divaricating stripes of white upon red background
<i>Jolonica nipponica</i>	2.5	bilacunar	nonbifurcate	divided hinge plates, with high crural-bases, hinge-sockets deep	present	conjunct	rose-red; some have intervening bands of light yellow mottling.
<i>Frenulina sanguinolenta</i>	1.5	bilateral	nonbifurcate	the cardinalia bear disjunct, inner hinge-plates elevated well above the valve floor	present	disjunct in small conjunct in large	yellowish brown with short irregular red stripes marginally
<i>Shimodaia pterygiota</i>	0.7	incomplete annular	nonbifurcate	steeply dipping inner hinge plates which converge on a low median septum	absent	disjunct	red-mottled, with intervening bands of white mottling.
<i>Terebratalia coreanica</i>	5.9	trabecular	bifurcate	callus between the socket-ridges joined to septum	present	conjunct	red with layers of white, rather dull
<i>Coptothyris grayi</i>	5.0	teloform	bifurcate	callus deposit between the socket-ridges with which septum unites	present	disjunct	dull red with radial ribs

**Shell shape and coloration.**—Externally, laqueoid species exhibit great variability in shell size and shape. In this study, it became apparent that the only external shell character that supported phylogenetic relationships was the pattern of shell coloration (Figure 5; top and second row). All the species in the clade of *Shimodaia-Frenulina-Pictothyris-Jolonica* exhibit irregular red stripes or mottling patterns, while shells of others are radially striped (in *L. rubellus* and *T. coreanica*) or have uniform coloration (in *C. grayi*, *L. blanfordi*, *L. quadratus*, *L. californicus* and *L. c. vancoveriensis*). Other external characters, such as the type of the commissure and completeness of deltidial plates, did not show any systematic distribution on the molecular phylogenetic tree.

**Adult loop morphology.**—The adult loop pattern is often thought to represent phylogenetic affinity among laqueoid genera, and has been used as a key character to divide the superfamily into families and subfamilies. For example, *Laqueus* and *Frenulina* have often been included in the same subfamily (Kingeninae in Richardson, 1975; Laqueinae in Smirnova, 1984) based on their possession of a bilateral adult loop. A close relationship between *Pictothyris* and *Laqueus* has also been maintained based on similarity of external characters, as well as adult loop patterns; the adult laterovertical loop of *Pictothyris* has been considered to be at a stage one step more advanced than that of *Laqueus* (see Thomson, 1927; Hatai, 1940; Smirnova, 1984).

However, the results of the molecular study suggest that these interpretations, based on adult loop morphology, are not reliable. The three genera possessing a bilateral, or laterovertical, adult loop (Figure 5; third row; boxed) did not form a clade, supporting the conclusion that a bilateral loop appeared independently in the lineage leading to *Laqueus* and *Frenulina*.

**Cardinalia.**—The cardinal process is prominent in most laqueoids; however, species belonging to the genera *Laqueus* and *Shimodaia* lack it. The molecular phylogenetic tree indicates that the cardinal process may have been lost at least twice independently (Figure 5; fourth row). *S. pterygiota* possesses steeply dipping inner hinge plates

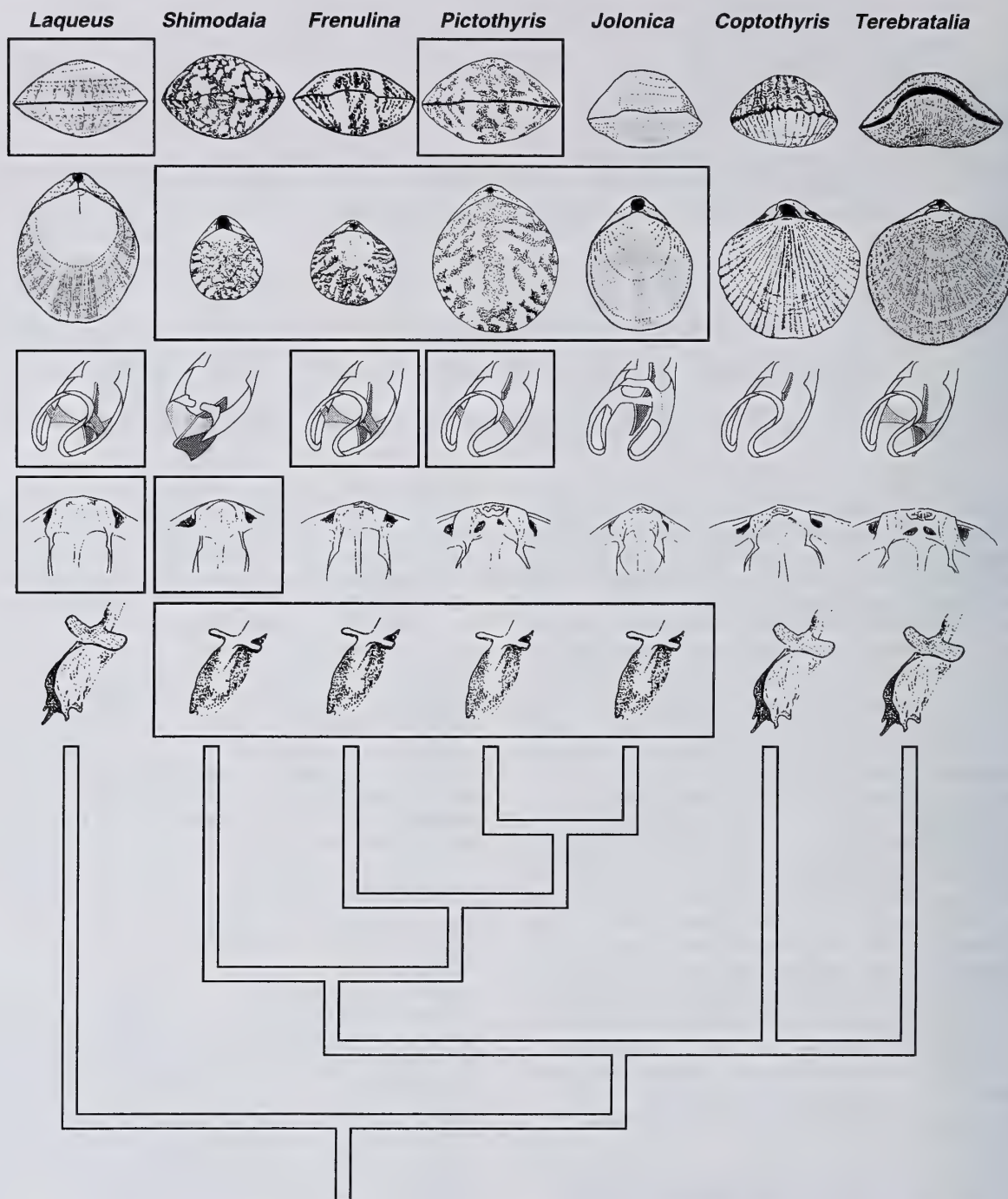
which converge on a low median septum to form a sessile septalium, comparable to that occurring in young *L. rubellus* and *Laqueus* sp. (Saito, 1996; MacKinnon *et al.*, 1997). This resemblance may also have resulted from parallel evolution.

**Juvenile loop morphology.**—At the axial phase of early loop development, when the median septum has a pair of flanges on its posterior part, the anterior part of the median septum bifurcates only in the basal species in the molecular phylogenetic tree, namely, *L. rubellus*, *C. grayi* and *T. coreanica* (Figure 5; fifth row). In all other species that form a clade, i.e., *F. sanguinolenta*, *P. picta*, *J. nipponica* and *S. pterygiota*, the septal pillar remain nonbifurcate until the annular phase (Figure 5; fifth row; boxed; Saito, 1996; MacKinnon *et al.*, 1997). Although the adult loop patterns may be misleading, early bifurcation of the septal pillar may be a useful character in assessing relationships among laqueoid genera.

## Discussion

### Laqueoid classification

Taxonomic assignments of the seven laqueoid genera investigated in this paper (*Laqueus*, *Terebratalia*, *Coptothyris*, *Shimodaia*, *Frenulina*, *Jolonica* and *Pictothyris*) have been controversial for a long time. Opinions as to which genera should be included in the family Laqueidae varied depending on the features that each author conjectured important. For example, Richardson (1973, 1975) considered the families Kingenidae, Macandreviidae and Laqueidae as synonymous, and proposed uniting them in the family Laqueidae, based on resorption patterns in loop development and the presence of dental plates. In this view, the seven ingroup genera compared in our molecular study are included in the family Laqueidae. Smirnova (1984) defined the Laqueidae as those with a loop of the late frenuliniform stage (i.e. bilacunar loop) or of more advanced stages, in which the connections between the ascending and descending branches remain joined to the septum at all stage. In so doing, she included a number of lower Cretaceous genera in the Laqueidae (*Zittellina*, *Zeuschneria*, *Tulipina*, *Waconella*),



**Figure 5.** Morphological characters of laqueoid species superimposed on the molecular phylogenetic tree. The tree topology represents the consensus of the Trees 1, 2, and 3 (cf. Figure 3). Vertical lengths of the branches are arbitrary. Morphological characters (from top to bottom): anterior view of the shells; dorsal view of the shells; adult loop pattern; cardinalia in the annular phase; septal pillar at the axial phase. The drawings are not strictly to scale. The rectimarginate commissure of *Laqueus* and *Pictothyris* (top row; boxed) which was previously considered to be evidence uniting these genera, appeared separately in the molecular phylogenetic tree. In the shell external features, the red-white dot coloration (second row; boxed) supports a close relationship between *Shimodaia*, *Frenulina*, *Pictothyris* and *Jolonica*. Characters such as the adult bilateral or latero-vertical loop pattern (third row; boxed), and the absence of cardinal process (fourth row; boxed), do not reflect phylogeny. The non-bifurcation of the septal pillar in the axial phase (bottom row; boxed) supports the *Shimodaia*-*Frenulina*-*Jolonica*-*Pictothyris* clade.



but excluded certain genera such as *Terebratalia* and *Coptothyris*, which exhibited a trabecular or teloform adult loop pattern. Zezina (1984) elevated the subfamily Terebrataliinae (Richardson, 1975) to family status, and distinguished it from the Laqueidae that accommodated such genera as *Laqueus*, *Frenulina*, *Aldingia*, *Jolonica*, *Pictothyris*, *Compso* and *Ecnomiosa*. More recently, in summarizing the biogeography of articulated brachiopods, Richardson (1997) included 13 living genera in the family Laqueidae (*Coptothyris*, *Jolonica*, *Pictothyris*, *Terebratalia*, *Laqueus*, *Tythyris*, *Simplicithyris*, *Frenulina*, *Ecnomiosa*, *Compso*, *Aldingia*, and two other undiscussed genera), but she did not provide explicit criteria for this classification.

Concerning the familial groupings of the seven Recent genera, the following two points can be drawn from the results of our *cox1* study. Firstly, in the rooted monophyletic cluster of laqueoids that included *Terebratalia* and *Coptothyris*, *Laqueus* branched off first, followed by a trichotomous cluster comprised of *Terebratalia*, *Coptothyris* and the subcluster of *Shimodaia*, *Frenulina*, *Jolonica*, and *Pictothyris* (Figure 5). Therefore, if *Terebratalia* and *Coptothyris* are excluded from the Laqueidae and included in the Terebrataliidae, then *Laqueus* and the remaining four genera (*Shimodaia*, *Frenulina*, *Jolonica*, and *Pictothyris*) should be accommodated in at least two separate families. A grouping including *Laqueus*, *Shimodaia*, *Frenulina*, *Jolonica*, and *Pictothyris* to the exclusion of *Terebratalia* and *Coptothyris* would be paraphyletic at best.

Secondly, in analyses of all the available terebratulid forms including other than laqueoids, *Ecnomiosa* branched off outside not only of the laqueoids, but also of the terebratuloids of the Southern Hemisphere (Saito et al., in press). Thus, on molecular grounds, the view of including *Ecnomiosa* in the family Laqueidae (Richardson, 1997) is not supported. MacKinnon and Gaspard (1996) reported that the descending branches of *Ecnomiosa* grow only from the crura unlike other long-looped brachiopods, justifying our conclusion based on loop ontogeny.

Inclusion of *Terebratalia* and *Coptothyris* and exclusion of *Ecnomiosa* imply that the adult loop morphology alone cannot be used as the prime character to define the Laqueoidea. Instead, presence of a pair of flanges on the septal pillar at the axial stage of loop ontogeny (Figure 8; Saito, 1996) and also the presence of dental plates in the ventral valve appear to be more explicit and better-suited character states to define this superfamily, and are to be incorporated as such in the diagnosis of the Laqueoidea in the forthcoming revised Treatise (MacKinnon, pers. comm., 2000).

### Processes of loop evolution

**Paedomorphosis.**— It is evident from comparison of the ontogenetic sequences of the loop morphology (Figure 6) with phylogenetic relationships (Figure 5), that paedomorphic loop evolution occurred at least twice among laqueoids, in the lineages that produced *Shimodaia* and *Jolonica*. As discussed in MacKinnon et al. (1997), adult individuals of *Shimodaia* have an incomplete annular loop, the brachidial ring being incomplete due to resorption of the very narrow transverse band. Adult individuals of *Jolonica* dis-

play a bilacunar loop, a loop with two pairs of connecting bands (lateral and mediovertical), although the width of the bands are different from that in the bilateral loop such as that found in *Laqueus*. The adult loop phases of both *Shimodaia* and *Jolonica* are comparable with juvenile loop phases in other laqueoid members, and based on the molecular cladograms (Figure 5), it is more parsimonious to consider the abbreviated ontogenies of *Shimodaia* and *Jolonica* as independent synapomorphies.

Williams and Hurst (1977) pointed out that the most significant trend within the post-Paleozoic long-looped terebratulids is the neotenus elimination of later stages of loop ontogeny and a simultaneous simplification of the lophophore. Our results indicate that such complex evolutionary processes have indeed been at work in laqueoids.

**Bifurcation.**— As reported by Richardson (1975) and Saito (1996), the loop ontogenies of laqueoid species appear to be roughly the same until the bilacunar phase. However, at the earlier axial phase, characterized by the development of septal flanges, two types of septal pillar can be recognized; in one form of septal pillar the anterior edge becomes bifurcate whereas in the other form of septal pillar the anterior edge is nonbifurcate (Saito, 1996; Figure 6). In *Laqueus* sp. (Figures 8.1, 8.2), *T. coreanica* (Figure 8.3) and *C. grayi* (Figure 8.4), the septal pillar is anteriorly bifurcate. On the other hand, *Pictothyris* sp. (Figure 8.5), *Jolonica nipponica* (Figure 8.6), *F. sanguinolenta* (Figure 8.7) and *Shimodaia pterygiota* (Figure 8.8) all exhibit a nonbifurcate septal pillar and retain remains of projections until the annular phase (Figure 9.5–9.8).

The results of molecular phylogeny indicate paraphyly for those with the bifurcate septal pillar (Figure 5). Thus, bifurcation is considered as the ancestral state and nonbifurcation a synapomorphy. Two Mesozoic laqueoid genera (*Gemmarcula* and *Trigonosemus*) show the anterior bifurcation of the septal pillar at the annular phase (Elliott 1947; Cooper 1955; Steinich 1965). This observation accords well with our contention that anterior bifurcation of the septal pillar is an ancestral character (Figure 5).

**Evolution of Bilateral Loop.**— As discussed earlier, the *cox1* results indicated that species with a bilateral adult loop did not form a monophyletic cluster (Figure 5). Two interpretations are possible for the evolution of the bilateral loop; one is that parallel evolution occurred, i.e., the bilateral loop evolved twice independently, and the other is that the bilateral loop is a plesiomorphic character.

The former interpretation tends to be supported by the fact that the two Cretaceous laqueoid genera, *Gemmarcula* and *Trigonosemus*, possess a trabecular loop. But the latter interpretation becomes equally possible if another genus such as *Waconella* from the Lower Cretaceous that has a bilateral loop in the adult phase is taken into consideration. *Waconella* has been considered as one of the members of the ancestral group from which *Laqueus* is derived, because of the possession of the same type of adult loop, cardinalia and shell shape, as well as the close geographical distribution with other laqueoid genera (Owen, 1970; Smirnova, 1984). Since a deep diversification between *Laqueus* and other laqueoid genera is inferred from the *cox1* analysis, this connection between *Waconella* and *Laqueus* seems quite

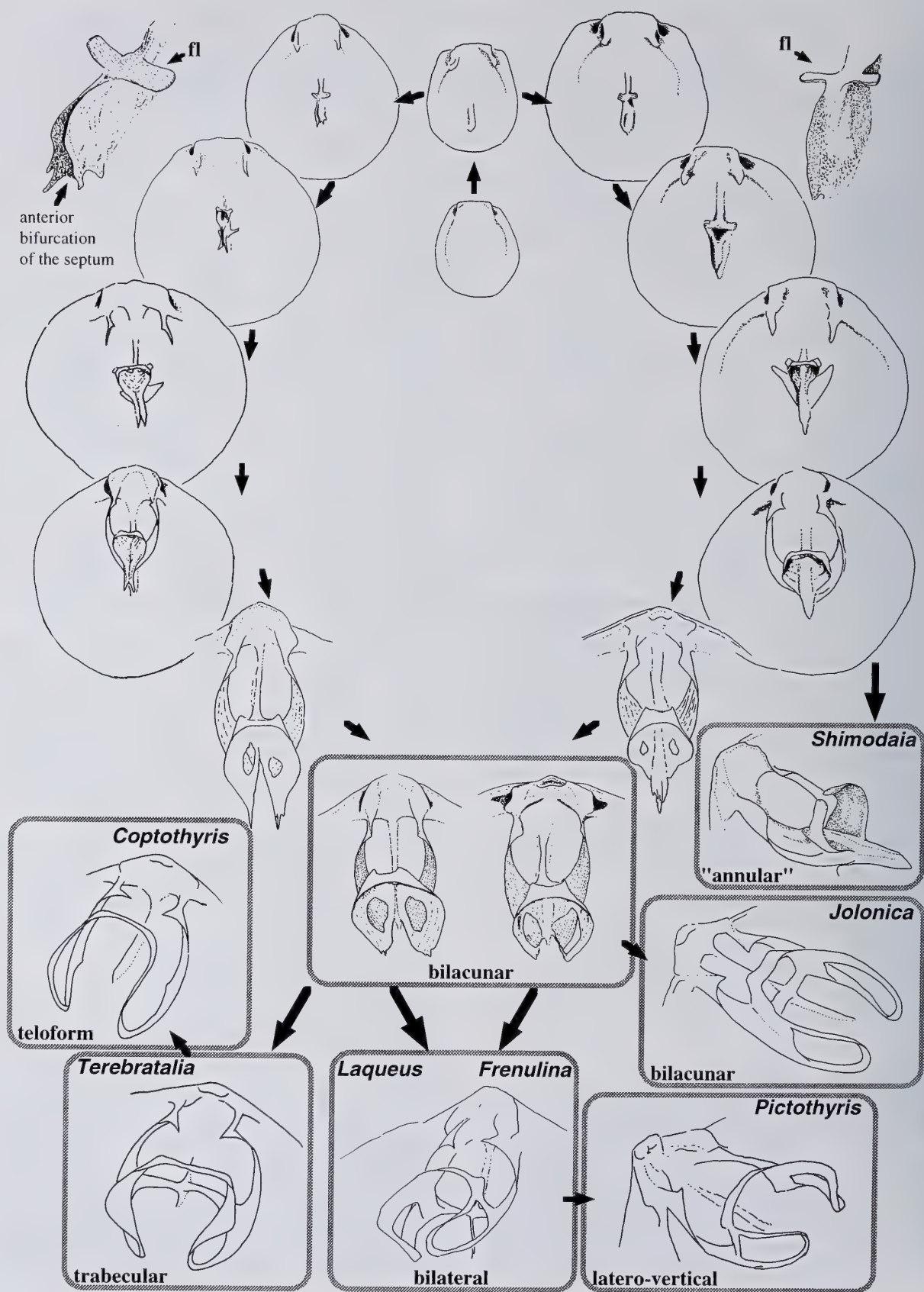


Figure 6.



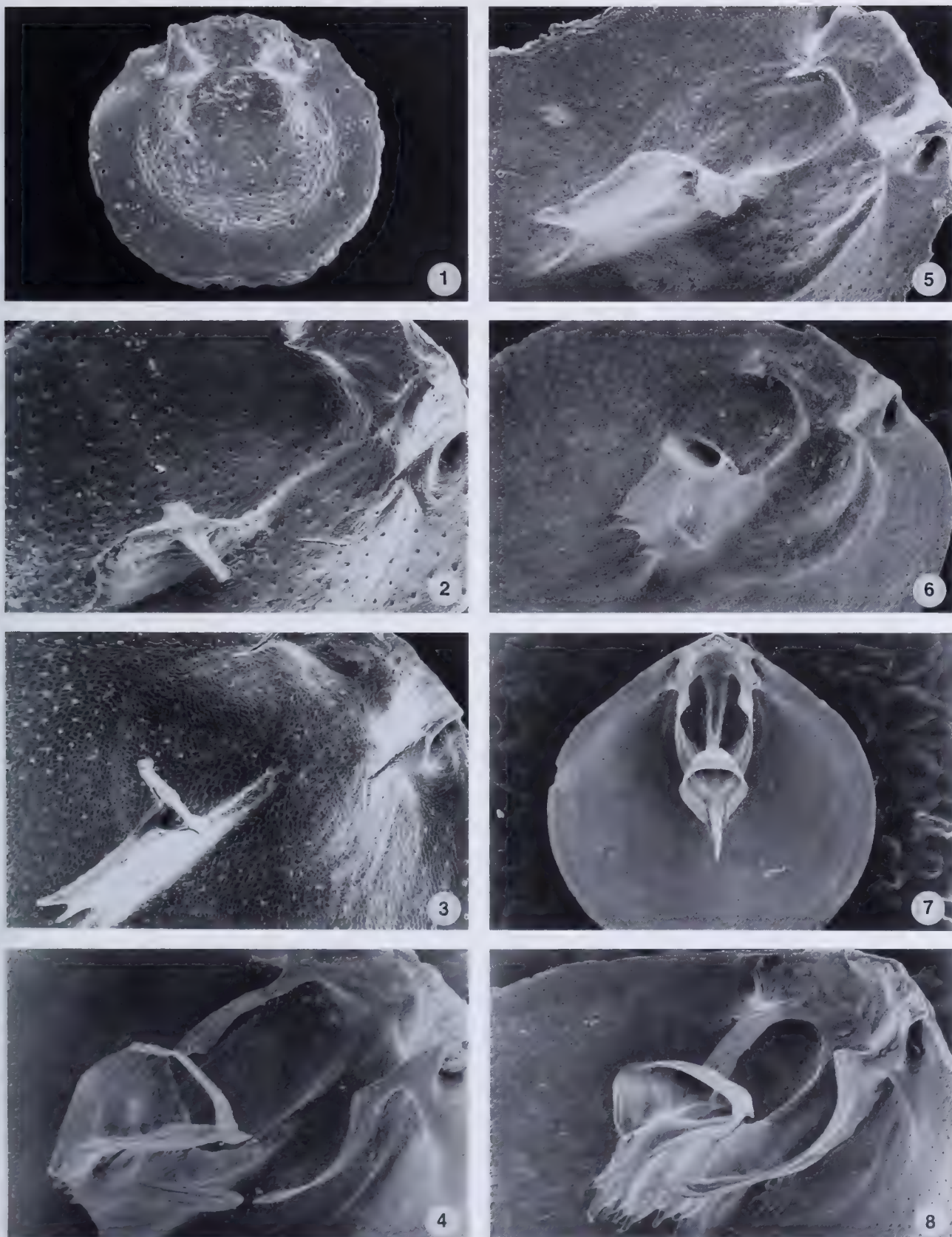


Figure 7.



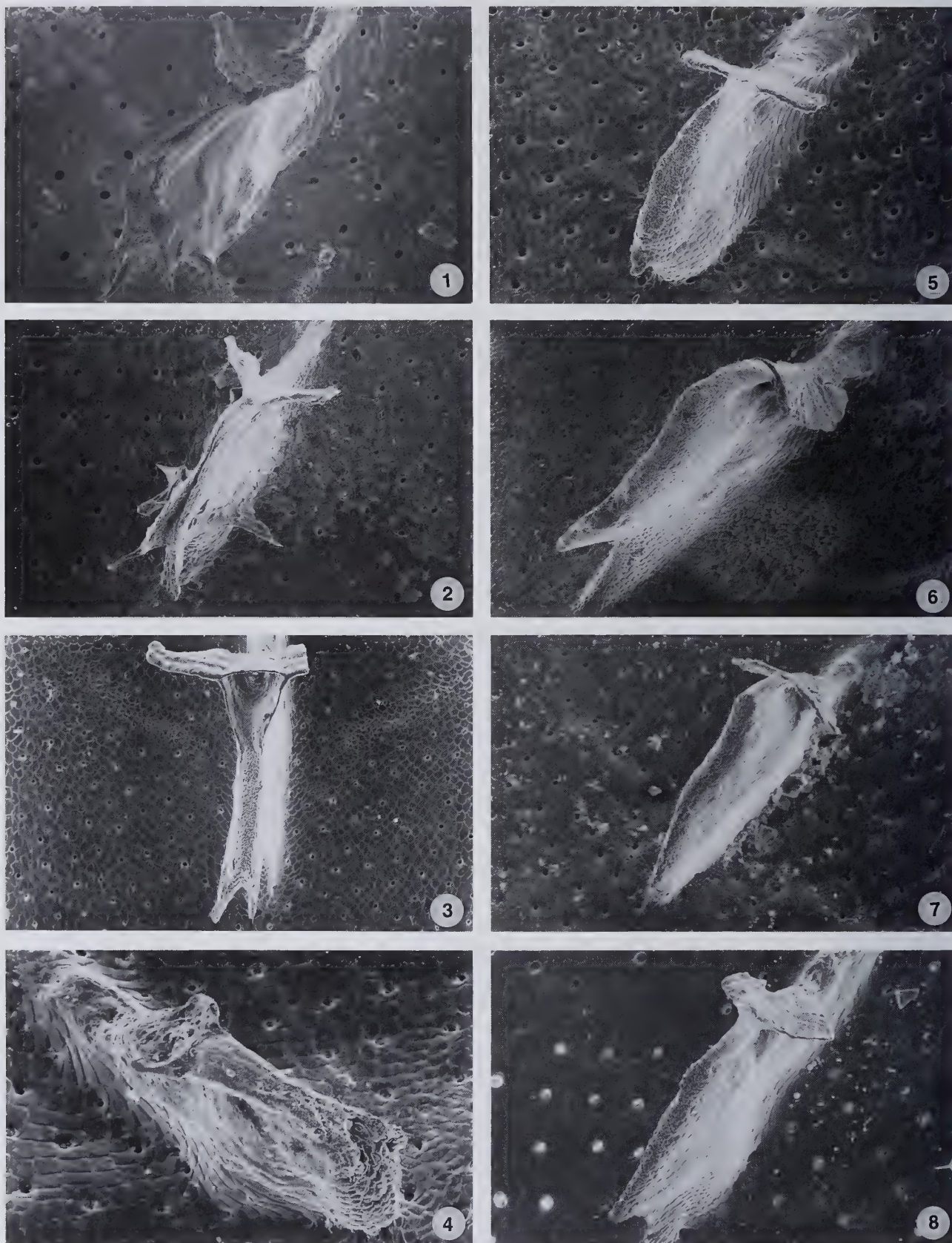


Figure 8.



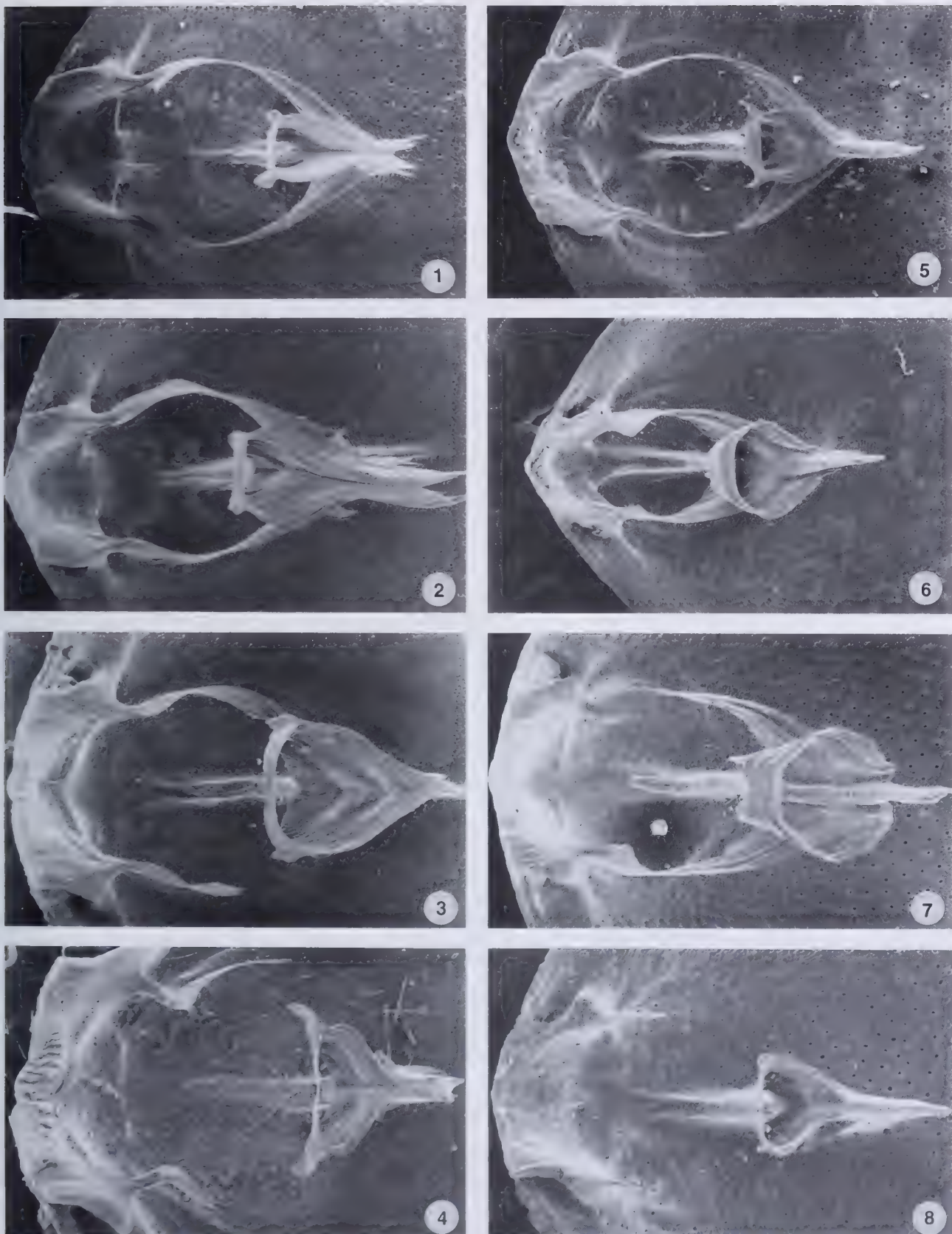


Figure 9.



probable, although the oldest fossil record of *Laqueus* is middle Miocene (Hatai, 1938). However, the early loop ontogeny of this genus is not reported, and it is not known whether *Waconella* has the laqueoid character of the flanges at the axial phase. The ancestral state of the laqueoid loop, therefore, cannot be established at present based on the morphology of fossil forms. The relationships of Mesozoic genera to the Cenozoic ones should become clearer when the early loop ontogenies, especially at the axial and annular phases of Mesozoic genera, are further examined.

### Conclusions

Molecular phylogenetic analysis using the *cox1* gene suggests that only a few morphological characters, such as coloration of the shell and bifurcation of the septal pillar, may be of use in deciphering the phylogenetic relationships of laqueoids. Other characters like cardinalia, external morphologies of the shell, notably, adult loop patterns, all of which have previously been considered as taxonomically important, are likely to have undergone a complex evolutionary history, and thus have to be treated with caution when used in taxonomic studies.

Reconstruction of the relationships of fossil and Recent terebratulide brachiopods is reliant mainly on the morphology of hard parts such as the shell, the loop and occasionally spicules, i.e., characters that can relatively easily be preserved in fossils. In addition, careful observations of

early loop development, especially of the fossil taxa, would be useful in filling existing gaps in the fossil record of the Laqueoidea and other superfamilies, and in resolving evolutionary relationships among fossil and Recent species. In any event, it appears important to evaluate the taxonomic value of each character, by means of molecular phylogeny of living species, to help clarify the phylogenetic history of terebratulide brachiopods and of other organisms in general.

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**Figure 6.** Loop ontogeny of the living laqueoid genera studied. Drawings are not to scale. The Laqueoidea is characterized by the presence of a pair of flanges (fl) on the septal pillar at the axial phase, and the patterns of ring resorption to produce the bilacunar loop pattern. The route to the bilacunar phase is two-fold; one with (left) and one without (right) anterior bifurcation of the median septum. The common bilacunar pattern for two types and adult patterns are boxed. Note that ontogenetic sequences to the adult patterns do not necessarily correspond with the phylogenetic relationships revealed by the molecular data.

**Figure 7.** Scanning electron microscopic images of early loop morphologies for *Terebratalia* and *Jolonica*. 1–4. *Terebratalia coreanica*. 1. Dorsal view, specimen UMUT RB28050 (L = 0.6 mm; L is the length of the dorsal valve), displays no loop-supporting structure (Prebrachidial phase),  $\times 77$ . 2. A specimen 1.5 mm in length shows septal flanges (Axial phase; oblique view), specimen UMUT RB28051,  $\times 63$ . The anterior part of the septal pillar is bifurcate. Cardinal process begins to develop during this stage. 3. Specimen UMUT RB28052 (L = 2.2 mm) displays a small hood with rudiments of the flanges,  $\times 48$ . Crura extend from areas at the base of the inner socket ridges. 4. Oblique view of the specimen UMUT RB28053 (L = 4.0 mm), showing the ring which retains the rudiments of the flanges (Annular phase),  $\times 32$ . The anterior part of the median septum is bifurcate. The descending branches extend further toward one another, albeit still unconnected. Further development of *Terebratalia coreanica* as those figured in Saito (1996). 5–8. *Jolonica nipponica*. 5. Lateral view of the smallest specimen UMUT RB28054 (L = 2.7 mm) displaying flanges (Axial phase),  $\times 37$ . Note that the ventral edge of the septal pillar is non-bifurcate. Crura project out from near the base of each inner socket ridge. 6. Posterodorsal view of the second smallest specimen UMUT RB28055 (L = 3.2 mm), showing a small hood, and small plates (future descending branches) on the septal pillar (Cucullate phase),  $\times 30$ . The crura and the descending branches extend further toward one another. 7–8. Annular phase. 7. Dorsal view of a larger specimen UMUT RB28056, (L = 3.8 mm) showing the annular phase loop and well developed cardinal process,  $\times 15$ . 8. Oblique view of the annular phase loop of the same specimen as in Fig. 8.6, showing the anteriorly spinose septal pillar and the ring with rudiments of the flanges. The septal pillar is spinous, but remains non-bifurcate,  $\times 31$ .

**Figure 8.** Comparison of the median septum morphology at the axial phase among laqueoid species. 1. *Laqueus* sp. (L = 1.9 mm), specimen UMUT RB28057,  $\times 155$ . 2. *Laqueus* sp. (L = 1.9 mm), specimen UMUT RB19819,  $\times 114$ . 3. *Terebratalia coreanica* (L = 2.2 mm), specimen UMUT RB28052,  $\times 73$ . 4. *Coptothyris grayi* (L = 1.3 mm), specimen 28498 in the collection of Tohoku University,  $\times 228$ . 5. *Pictothyris* sp. (L = 1.5 mm), specimen UMUT RB19830,  $\times 113$ . 6. *Jolonica nipponica* (L = 2.7 mm), specimen UMUT RB28054,  $\times 63$ . 7. *Frenulina sanguinolenta* (L = 2.0 mm), specimen UMUT RB28058,  $\times 77$ . 8. *Shimodaia pterygiota* (L = 1.54 mm), specimen UMUT RB28059,  $\times 120$ .

**Figure 9.** Comparative views of cardinalia at the annular phase in eight laqueoid species. 1. *Laqueus* sp. (L = 2.7 mm), specimen UMUT RB19821,  $\times 39$ . 2. *Laqueus blanfordi* (L = 3.7 mm), specimen UMUT RB28060,  $\times 30$ . 3. *Terebratalia coreanica* (L = 4.0 mm), specimen UMUT RB28053,  $\times 30$ . 4. *Coptothyris grayi* (L = 2.3 mm), specimen UMUT RB28061,  $\times 31$ . 5. *Pictothyris* sp. (L = 2.5 mm), specimen UMUT RB19836,  $\times 37$ . 6. *Jolonica nipponica* (3.8 mm), specimen UMUT RB28056,  $\times 24$ . 7. *Frenulina sanguinolenta* (L = 3.9 mm), specimen UMUT RB28062,  $\times 30$ . 8. *Shimodaia pterygiota* (L = 2.2 mm), specimen UMUT RB28063,  $\times 48$ .



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# The genus *Hourcquia* (Ammonoidea, Pseudotissotiidae) from the Upper Cretaceous of Hokkaido, Japan: biostratigraphic and biogeographic implications

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**Abstract.** Stratigraphic and ontogenetic descriptions of three species of *Hourcquia* from the Cretaceous Yezo Supergroup of Hokkaido, Japan are given for the first time. *H. ingens*, *H. hataii* and *H. kawashitai* occur in the *Inoceramus teshioensis* Zone of the upper Turonian. *Hourcquia* evolved and radiated in not only the Tethyan and adjacent areas but also the Northwest Pacific region for a short period in the late Turonian.

**Key words:** Ammonoid, Hokkaido, *Hourcquia*, late Turonian, Yezo Supergroup

## Introduction

The genus *Hourcquia* Collignon, 1965 of the family Pseudotissotiidae is characterized by having trapezoidal whorl sections with a rounded keel, coarse ribs, and umbilical and ventrolateral tubercles. Species of the genus are known to occur from the upper Turonian of Madagascar (Collignon, 1965), Venezuela (Renz, 1982), New Mexico, and Texas (Anonymous, 1981). These areas belong to the Tethyan and surrounding realms.

Distribution of the present genus extends also to the northwest Pacific region. Five species of *Hourcquia* are known from the Cretaceous Yezo Supergroup of Hokkaido, Japan (Hashimoto, 1973; Matsumoto and Obata, 1982; Matsumoto and Toshimitsu, 1984; Toshimitsu and Maiya, 1986) and Sakhalin, Russia (Matsumoto, 1970). However, no detailed analysis has been undertaken of their exact stratigraphic occurrences and variations of shell growth. Further work based on better material is desirable for elucidating the ontogeny, biostratigraphy and biogeography of the genus.

Recently, we collected several well-preserved specimens referable to *Hourcquia* from the Cretaceous Yezo Supergroup in the Ikushumbetsu, Miruto and Haboro areas, Hokkaido (Figure 1). In this paper, we describe three species of the genus and discuss their biostratigraphic and

biogeographic implications.

## Note on stratigraphy

The Cretaceous Yezo Supergroup consists of clastic deposits in a forearc basin. The supergroup is widely distributed in the median zone of Hokkaido (Figure 1) and is divided into four groups, the Lower Yezo, Middle Yezo, Upper Yezo and Hakobuchi groups in ascending order (Okada, 1983).

## Ikushumbetsu and Miruto areas

The Middle and Upper Yezo groups, ranging from the Albian to Santonian stages, are exposed along the Ikushumbetsu and Horomui rivers and their tributaries. The Middle Yezo Group is subdivided into the lower-lying 'Main Part' (Matsuno *et al.*, 1964) and the Mikasa Formation (Matsumoto, 1951). The former consists of well-bedded sandstone or laminated mudstone with sandstone intercalations. The latter consists mainly of sandstone exhibiting hummocky cross-stratification; it is subdivided into four units, Ta of sandstone, Tb of sandstone to muddy sandstone, Tc of mudstone, and Td of sandstone to muddy sandstone, in ascending order (Matsuno *et al.*, 1964). The Upper Yezo Group consists mainly of sandy mudstone in the lower part and homogenous fine-grained mudstone in the

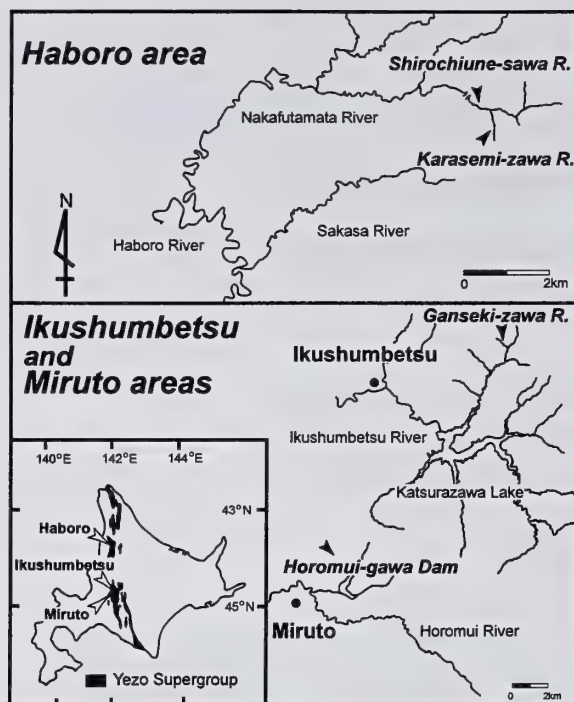


Figure 1. Maps of the Haboro and Ikushumbetsu-Miruto areas showing the localities of the *Hourcquia* species examined.

upper part. The group conformably overlies the Mikasa Formation, although the lithologic boundaries are diachronous (Ando, 1990).

The specimen assigned to *Hourcquia ingens* was obtained from the lower part of the Upper Yezo Group along the Ganseki-zawa, a stream of the Ikushumbetsu River (Figure 1). This part consists mainly of intensively bioturbated sandy mudstone with intercalations of discontinuous sandstone beds, interpreted as distal storm-sheets on the outer shelf. That specimen is associated with *Subprionocyclus minimus* and *Inoceramus teshioensis* (Figure 2), which are diagnostic fossils of the upper part of the upper Turonian (see Toshimitsu *et al.*, 1995).

The specimen assigned to *Hourcquia kawashitai* was found in the unit Td of the Mikasa Formation, composed of muddy bioturbated sandstone of inner-shelf type, near the Horomui-gawa Dam of the Miruto area. Ando (1990) refers the stratigraphic level of the locality to the upper Turonian.

#### Haboro area

The Middle and Upper Yezo groups, ranging from the middle Turonian to lower Campanian stages, are exposed in the upper reaches of the Haboro River. The Shirochi Formation of the Middle Yezo Group consists of mudstone with intercalations of thin turbidite-sandstone beds (Toshimitsu, 1985). The Upper Yezo Group conformably overlies the Shirochi Formation and consists mainly of mudstone in the lower part and mudstone with intercalations of thin sandstone in the middle part, while the upper part coarsens upward, beginning with mudstone and ending with cross-bedded sandstone (Toshimitsu, 1985).

The specimens determined as *Hourcquia hataii* were extracted from calcareous concretions in float along the Shirochiune-sawa and Karasemi-zawa valleys. The Shirochi Formation of offshore mudstone is distributed in this area and correlated with the *Inoceramus teshioensis* Zone of the upper Turonian (Toshimitsu and Maiya, 1986). Those specimens were found associated with *Subprionocyclus neptuni* and *Inoceramus teshioensis* in the concretions.

**Repository of specimens.**—The specimens described and figured herein are reposit in the National Science Museum, Tokyo with prefix of NSM PM and in the Institute of Geoscience, University of Tsukuba (formerly the Institute of Geology and Mineralogy, Tokyo University of Education) with prefix of TKU.

**Abbreviations.**—D = shell diameter; NSM PCL = National Science Museum, Paleontological Collection Locality.

#### Systematic descriptions

Superfamily Acanthoceraoidea Grossouvre, 1894

Family Pseudotissotiidae Hyatt, 1903

Subfamily Hourcquinae Renz, 1982

Genus *Hourcquia* Collignon, 1965

**Type species.**—*Hourcquia mirabilis* Collignon, 1965.

*Hourcquia ingens* Collignon, 1965

Figures 3a–d, 4, 5

*Hourcquia ingens* Collignon, 1965, p. 80, pl. 412, figs. 1704–1706, pl. 413, fig. 1708; Matsumoto and Obata, 1982, p. 79, pl. 4, fig. 2a–c.

*Hourcquia ingens* var. *antsakoazatensis* Collignon, 1965, p. 82, pl. 413, figs. 1707, 1710.

**Type.**—Holotype is the original of Collignon (1965, p. 80, pl. 412, fig. 1704), from the Masiaposa area, Madagascar.

**Material.**—One specimen, NSM PM16159. Shell moderately large, 110 mm in D at preserved last septum, and consists of only phragmocone.

**Locality.**—NSM PCL 4–15–3 [= Loc. 319 in Futakami (1986)]: a cliff along Ganseki-zawa, a tributary of the Kami-ichino-sawa River in the Ikushumbetsu area, Hokkaido (Figure 1).

**Description.**—Coiling moderately involute, with fairly narrow and deep umbilicus, rounded umbilical shoulder, and gently convex to nearly vertical umbilical wall. Shell surface ornamented, more distinctively on inner whorls, with prorsiradiate ribs tuberculated at umbilical and ventrolateral shoulders, springing in pairs from umbilical tubercles and intercalated shorter ones. Whorl cross-section subtrapezoidal on inner whorls and subtriangular on outer preserved whorl, with maximum breadth at umbilical tubercles; rounded keel on fastigate venter, obtuse ventrolateral shoulder. Lateral lobe of suture line asymmetrically divided and deeply incised (Figure 5).

**Comparison.**—The immature shell described as *Hourcquia ingens* by Matsumoto and Obata (1982, pl. 4, fig. 2a–c) from Hokkaido is more involute than our specimen



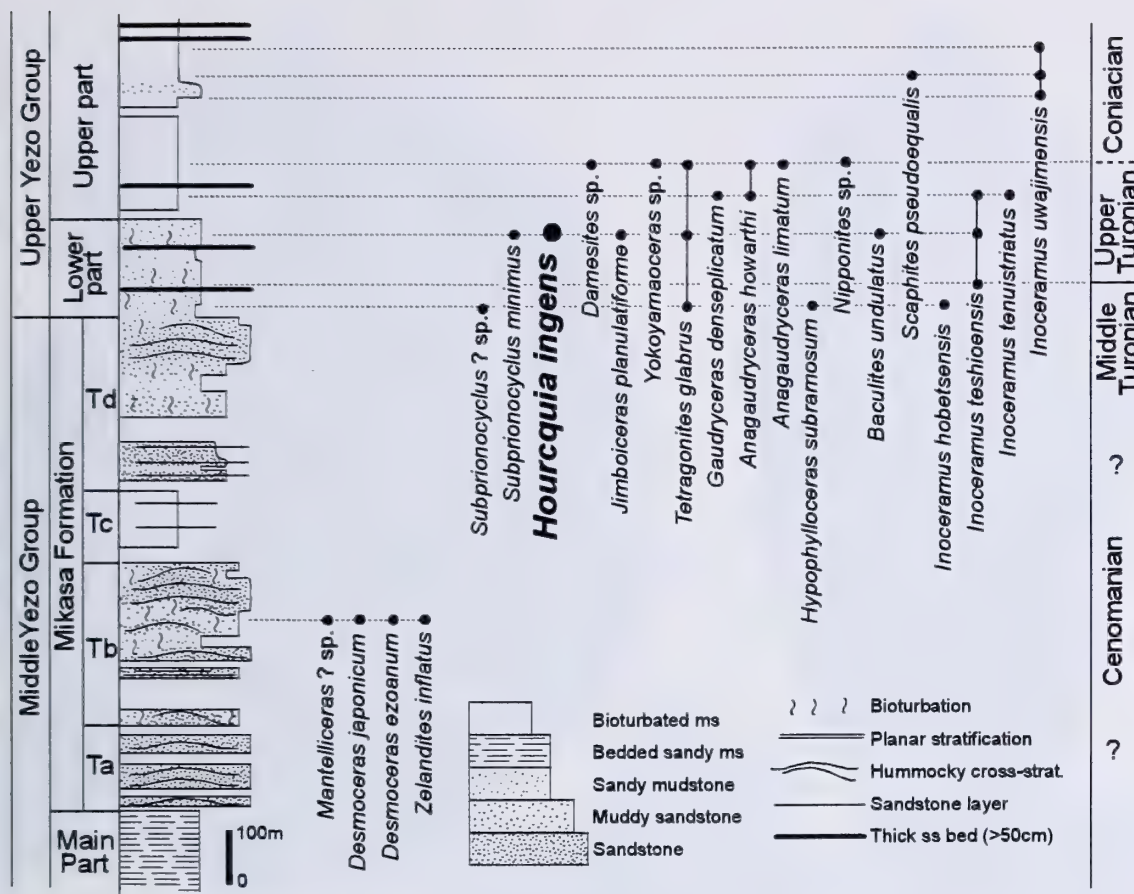


Figure 2. Columnar section and stratigraphic distribution of ammonoids and inoceramids along the Ganseki-zawa Valley, Ikushumbetsu. *Hourcquia ingens* Collignon occurs from the lower part of the Upper Yezo Group, in association with *Subprionocyclus minimus* (Hayasaka and Fukada), an index ammonite of the uppermost part of the upper Turonian in Japan.

NSM PM16159. The specimens from Madagascar display wide variation in the width of the umbilicus during the immature growth-stage (Collignon, 1965, figs. 1705, 1706, 1708, 1710). Both specimens from Japan are included in the range of variation for the species.

*Hourcquia ingens* closely resembles *Hourcquia moralesi* Renz (1982, p. 104, pl. 34, fig. 2) from the upper Turonian of Venezuela in having a subtriangular whorl section and bifurcated, intercalated and projected ribs. The latter is, however, distinguished from the former in retaining the ornamentation until a late growth-stage.

**Occurrence.**—Upper Turonian, *Coilopoceras requieni-Romaniceras deveriai* Zone in Madagascar. Upper part of the upper Turonian, *Subprionocyclus minimus* Subzone of *Inoceramus teshioensis* Zone in Hokkaido, Japan.

#### *Hourcquia hataii* Hashimoto, 1973

Figure 6a-j, 7, 8

*Hourcquia hataii* Hashimoto, 1973, p. 316, pl. 35, text-fig. 2.

**Type.**—Holotype (TKU30492), by monotypy, is the specimen figured by Hashimoto (1973, pl. 35) from the

Nigorikawa River (Loc. 6373114p) in the Teshio area, northern Hokkaido.

**Material.**—Two specimens extracted from calcareous concretions in float along the Shirochiune-sawa Valley and its small tributary, the Karasemi-zawa Valley, in the Haboro area, Hokkaido are used in the following description: NSM PM16161, from the same place as Loc. RH2096 in Toshimitsu (1985), consists mainly of phragmocone of 70 mm in D at depressed apertural part; NSM PM16162, from the lower course of the Karasemi-zawa Valley, 30 mm in D at compressed apertural part.

**Description.**—Shell displays large ontogenetic variation (Figures 6a-j). In initial growth-stage (D < 5 mm), shells involute with depressed whorl section. Immature (5 < D < 50 mm), shells evolute with, firstly, compressed whorl section and less ornamentation on shell surface, and, later, subtrapezoidal whorl section, rounded keel, bifurcated and intercalated ribs, and ventral and umbilical bullae. At later growth-stage (D > 50 mm), shell involute with steep umbilical wall; whorl cross-section then subtrapezoidal with strong ventrolateral and umbilical tubercles and rounded broad keel.

Initial chamber elliptical in median section (Figure 7),



**Figure 3.** a-d. *Hourcquia ingens* Collignon, NSM PM16159, from NSM PCL 4-15-3 [= the locality 319 in Futakami (1986)], Ikushumbetsu,  $\times 1.0$ . c, d. Inner whorls of a and b. Note the change of shell shape and ornamentation through growth. Dimensions for each growth-stage observed at the solid arrows. b; D (shell-diameter) = 104.0 mm, U (umbilical-diameter) = 25.1 mm, B (whorl-breadth) = 53.6 mm, H (whorl-height) = 47.5 mm; d; D = 65.5 mm, U = 16.8 mm, H = 27.0 mm. e. *Subprinocyclus minimus* (Hayasaka and Fukada), NSM PM16163, from NSM PCL 4-15-3, Ikushumbetsu,  $\times 1.2$ .



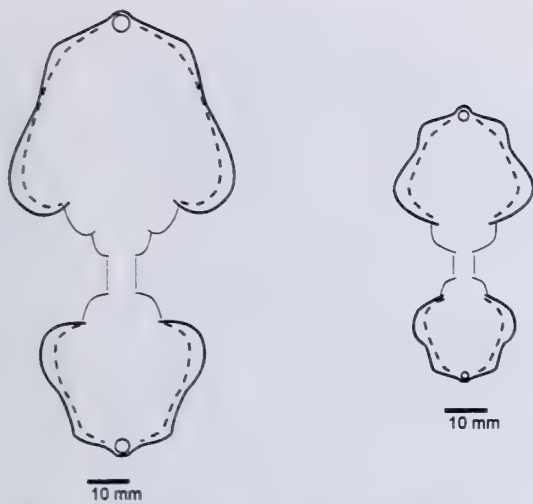


Figure 4. Median cross sections of *Hourcquia ingens* Collignon, NSM PM16159 showing the ontogenetic change of whorl-shape (right to left). The dashed line shows the intercostal whorl cross-section.

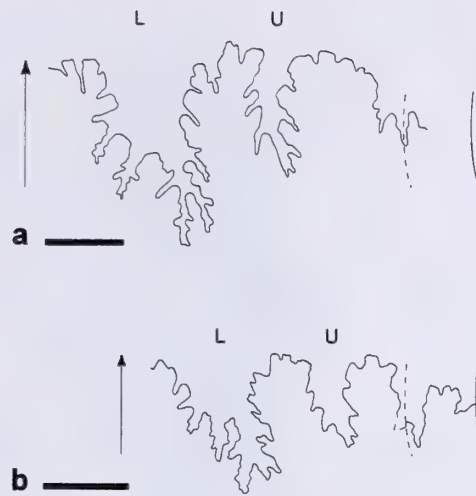


Figure 5. Suture line of *Hourcquia ingens* Collignon, NSM PM16159. a. Whorl-height = 24.4 mm. b. Whorl-height = 21.3 mm. Scale bars = 5.0 mm. L; lateral lobe, U; umbilical lobe.

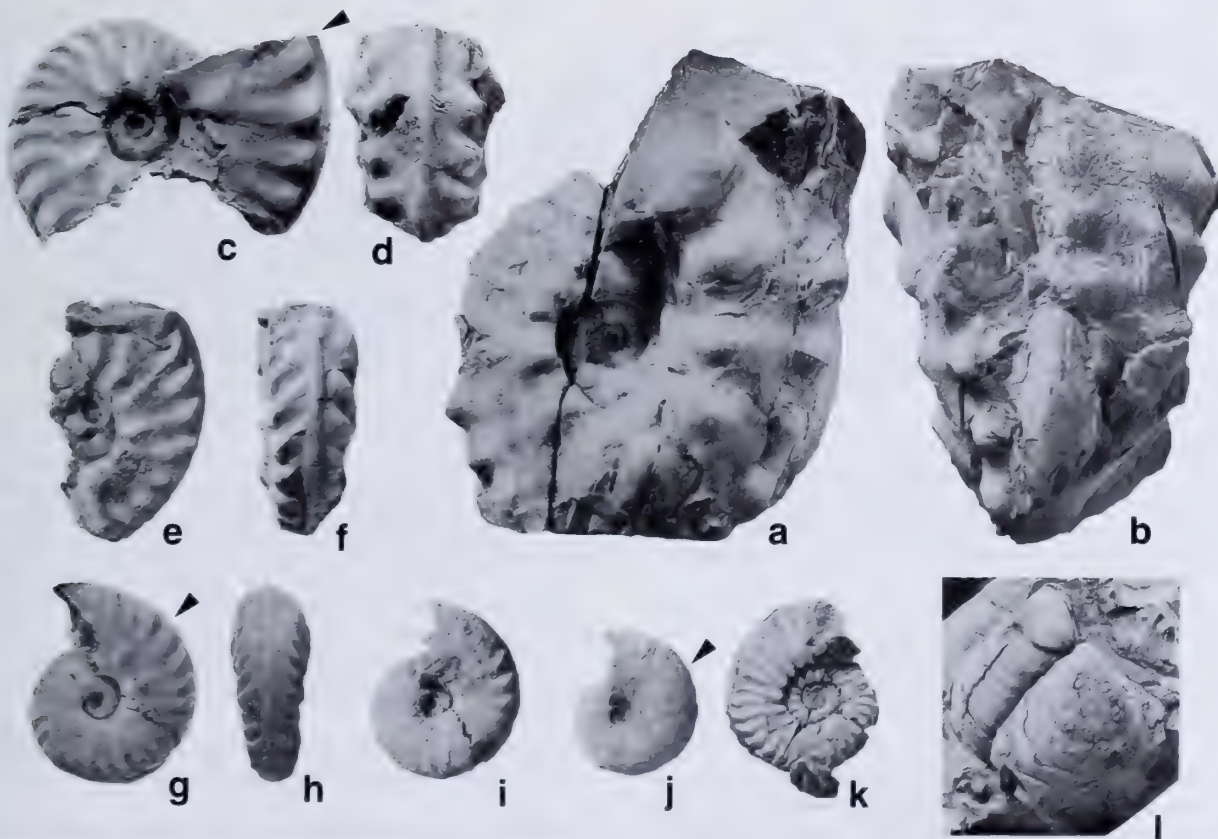
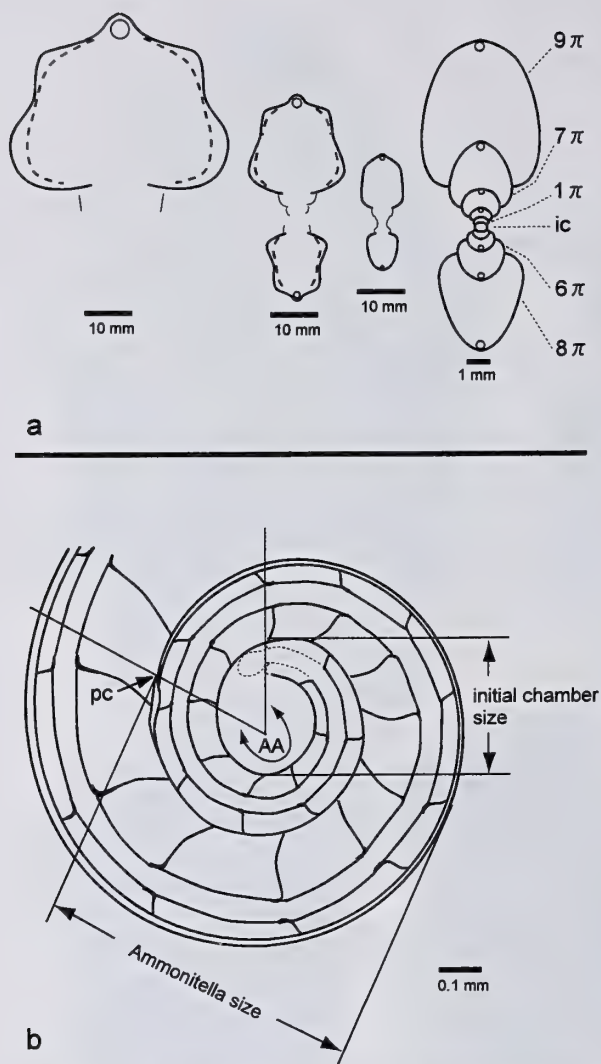


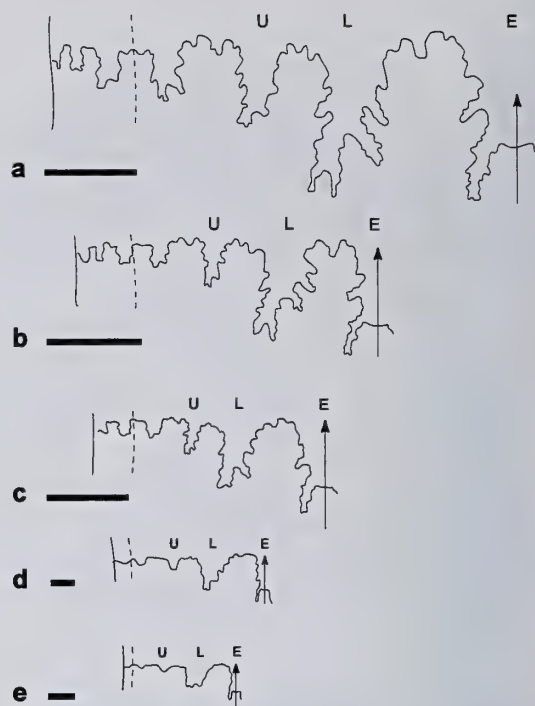
Figure 6. a-j. *Hourcquia hataii* Hashimoto. a, b. NSM PM16161, from the Shirochiune-sawa River,  $\times 1.0$ . c, d. Inner whorls of a and b [NSM PM16161],  $\times 1.0$ . e, f. NSM PM16162, from the Karasemi-zawa River,  $\times 1.0$ . g, h. Inner whorls of a and b [NSM PM16161],  $\times 1.0$ . i, j. Inner whorls of a and b [NSM PM16161],  $\times 1.2$ . Note the change of shell-shape and ornamentation throughout growth. Dimensions for each growth-stage observed at the solid arrows. c; D = 43.0 mm, U = 8.5 mm, B = 20.2 mm, H = 20.2 mm; g; D = 23.4 mm, U = 5.7 mm, B = 9.2 mm, H = 10.6 mm; j; D = 12.7 mm, U = 2.7 mm, B = 5.8 mm, H = 6.0 mm. k. *Subprionocyclus neptuni* (Geinitz), NSM PM16164, associated with NSM PM16162,  $\times 1.2$ . l. *Inoceramus teshioensis* Nagao and Matsumoto, NSM PM16165, associated with NSM PM16161,  $\times 1.2$ .



**Figure 7.** a. Median cross sections of *Hourcquia hataii* Hashimoto, NSM PM16161 showing the ontogenetic change in whorl-shape (right to left). The dashed line shows the intercostal whorl cross-section. Angles for whorl-diameter are measured from the base of the caecum (see b). *ic*; initial chamber. b. Early internal shell structure of *Hourcquia hataii*, NSM PM16161 showing measurements of initial chamber size, ammonitella size, and ammonitella angle (AA). The ammonitella angle is defined as the angle from the base of the caecum to the primary constriction (pc).

measuring 0.46 mm in diameter. Siphuncular tube occupying subcentral position in first whorl and subsequently moving towards ventral side in second whorl. Ammonitella size and angle in median section 0.78 mm and  $303^\circ$  respectively. Lateral lobe of suture line asymmetrically divided and deeply incised (Figure 8).

**Comparison.** — *Hourcquia hataii* closely resembles *Hourcquia mirabilis* from Madagascar (Collignon 1965, p. 77, fig. 1703) and *H. krausei*, monotypic, from Venezuela (Renz 1982, p. 104, pl. 34, fig. 1) in respect of the strong



**Figure 8.** Suture line of *Hourcquia hataii* Hashimoto, NSM PM16161. a. Whorl-height = 20.5 mm. b. Whorl-height = 14.1 mm. c. Whorl-height = 10.3 mm. d. Whorl-height = 5.7 mm. e. Whorl-height = 4.0 mm. Scale bars for a-c = 5.0 mm, for d, e = 1.0 mm. E; external lobe, L; lateral lobe, U; umbilical lobe.

ventrolateral and umbilical tubercles on the subtrapezoidal whorl in the later growth-stage. The latter two are distinguished from the former in having a concavely impressed spiral band on the flank.

**Discussion.** — The monotypic holotype of *Hourcquia hataii* was extracted from a calcareous concretion in float without any age-diagnostic information; Hashimoto (1973) interpreted the horizon as being Coniacian. We found two specimens referable to *H. hataii* together with *Inoceramus teshioensis* and *Subprionocyclus neptuni* (Figure 6k, l) in the same concretions. Since the latter is diagnostic of the Upper Turonian, we revise the stratigraphic occurrence of the present species to within the Upper Turonian.

**Occurrence.** — Upper Turonian, *Inoceramus teshioensis* Zone, Hokkaido, Japan.

#### *Hourcquia kawashitai* Matsumoto and Toshimitsu, 1984

Figures 9–12

*Hourcquia kawashitai* Matsumoto and Toshimitsu, 1984, p. 233, pl. 32, figs. 1, 2; pl. 33, figs. 1–3; pl. 34, fig. 2, text-figs. 2, 3.

**Type.** — Holotype, YKC.57–6–20–E, Y. Kawashita's Collection, is the original of Matsumoto and Toshimitsu (1984, pl. 32, fig. 1), from the Karasemi-zawa Valley in the Haboro area, northwestern Hokkaido (Figure 1).

**Material.** — One specimen, NSM PM16160. Immature





**Figure 9.** *Hourcquia kawashitai* Matsumoto and Toshimitsu, NSM PM16160, from NSM PCL 4-14-15, Miruto,  $\times 1.0$ . **c-f.** Inner whorls of a and b. Dimensions for each growth stage observed at the solid arrows. a; D = 81.3 mm, U = 9.2 mm, B = 28.5 mm, H = 40.5 mm; c; D = 49.7 mm, U = 4.9 mm, B = 19.0 mm, H = 25.0 mm; e; D = 25.1 mm, U = 2.9 mm, B = 9.8 mm, H = 13.1 mm. The white arrow shows the location of the last suture-line.

shell, 82 mm in D, and consists of phragmocone and long body chamber occupying about  $270^\circ$  in spiral length, without complete aperture.

**Locality.**—NSM PCL 4-14-15: a cliff about 2 km north of the Horomui-gawa Dam in the Miruto area, Hokkaido (Figure 1).

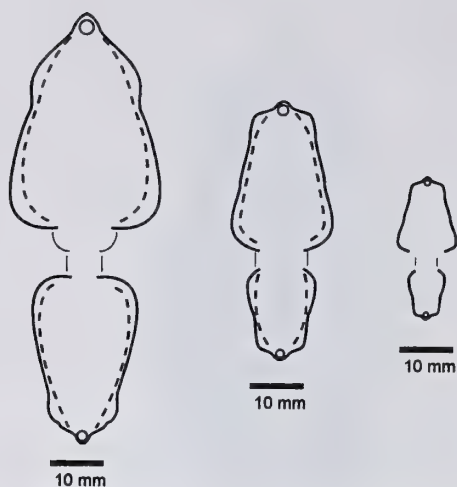
**Description.**—Coiling very involute, with narrow and deep umbilicus, rounded umbilical shoulder and nearly vertical umbilical wall. Shell surface ornamented with prorsiradiate ribs tuberculated at umbilical and ventrolateral shoulders, springing in pairs from umbilical tubercles and with intercalated shorter ones. Ribs weaker on flank. Whorl cross-section high subtriangular with maximum breadth at umbilical tubercles, rounded keel on roof-shaped venter, obtuse

ventrolateral shoulder.

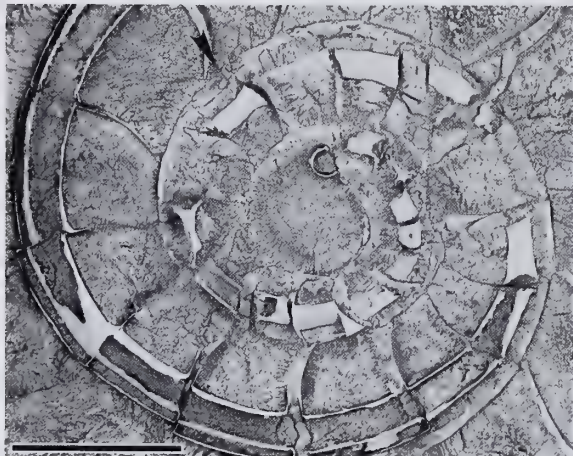
Initial chamber elliptical in median section, measuring 0.42 mm in diameter. Caecum subelliptical in lateral view (Figure 11). Prosiphon not preserved. Siphuncular tube occupies subcentral position in first whorl and gradually moves toward ventral side in second whorl. Ammonitella size and angle in median section, 0.89 mm and  $310^\circ$ , respectively. Lateral lobe of suture line asymmetrically divided and deeply incised (Figure 12).

**Comparison.**—Although the specimen NSM PM16159 is an immature shell, the shape and ornament are essentially the same as those of the inner whorl of *Hourcquia kawashitai* (Matsumoto and Toshimitsu, 1984; pl.32, fig.2).

**Occurrence.**—Upper Turonian, *Inoceramus teshioensis*



**Figure 10.** Median cross sections of *Hourcquia kawashitai* Matsumoto and Toshimitsu, NSM PM16160 showing the ontogenetic change in whorl-shape (right to left). The dashed line shows the intercostal whorl cross-section.

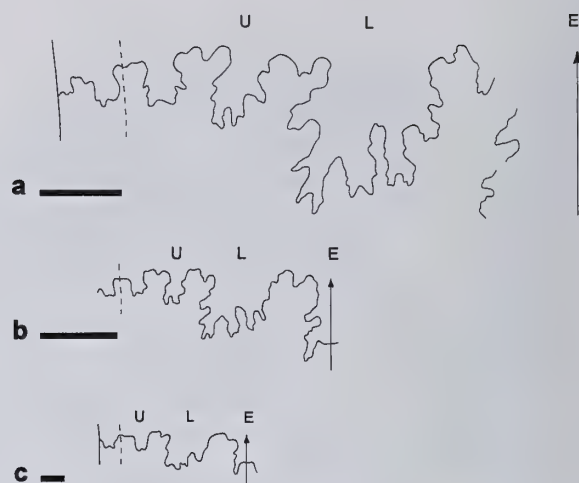


**Figure 11.** SEM micrograph of the early internal shell structure of *Hourcquia kawashitai* Matsumoto and Toshimitsu, NSM PM16160, in median section. The arrow shows the primary constriction. Scale bar = 0.5 mm. See Figure 7-B for measurements of initial chamber size, ammonitella size, and ammonitella angle.

Zone in Hokkaido, Japan.

### Discussion

Five species of *Hourcquia*, *H. mirabilis*, *H. ingens*, *H. pacifica*, *H. hataii* and *H. kawashitai*, have been described up to now from the Cretaceous of Hokkaido and Sakhalin. Almost all species were not collected *in situ* but from calcareous concretions in float without specific stratigraphic evidence. Previous authors thought that the biostratigraphic horizon of *H. hataii* was the Coniacian, that of *H. pacifica* was the upper Turonian to Coniacian, and that of the other



**Figure 12.** Suture line of *Hourcquia kawashitai* Matsumoto and Toshimitsu, NSM PM16160. **a.** Whorl height = 28.6 mm. **b.** Whorl height = 14.0 mm. **c.** Whorl height = 9.3 mm. Scale bars for **a**, **b** = 5.0 mm, for **c** = 1.0 mm. E; external lobe, L; lateral lobe, U; umbilical lobe.

three species was the upper Turonian. In this paper, we have determined the precise biostratigraphic horizons of the following three species. *H. ingens* occurred in the upper part of the upper Turonian associated with *Subprionocyclus minimus*, *H. hataii* occurred in the Upper Turonian with *S. neptuni*, and *H. kawashitai* was also obtained from the upper Turonian. In the Tethyan and adjacent regions, *Hourcquia* radiated only during the late Turonian; *H. mirabilis* and *H. ingens* in Madagascar (Collignon, 1965), *H. krausi* and *H. moralesi* in Venezuela (Renz, 1982), *H. cf. mirabilis* in New Mexico and Trans-Pecos Texas (Anonymous, 1981). In consequence the genus *Hourcquia* seems to be useful for inter-regional biostratigraphic correlation.

In Hokkaido and Sakhalin, it is generally considered that the ammonoid fauna is characteristic of the North Pacific bio-province, different from both the Tethyan and Boreal provinces, during the post-Albian. However, the occurrence of *Hourcquia* species in the Yezo Supergroup, including two pandemic ones, *H. mirabilis* and *H. ingens* and three endemic ones, *H. pacifica*, *H. hataii*, and *H. kawashitai*, demonstrates that this genus evolved and radiated in not only the Tethyan and adjacent regions but also possibly in the northwest Pacific region for a short period in the late Turonian. In a similar manner, the Tethyan vascoceratids entered into the Yezo forearc basin for a short period in the early Turonian (Matsumoto, 1973; Matsumoto, 1978; Matsumoto and Muramoto, 1978). The oxygen isotope evidence suggests two cycles of rapid warming during earliest Turonian and middle to late Turonian time (Jenkyns *et al.*, 1994; Clarke and Jenkyns, 1999). The extended distributions of *Hourcquia* and vascoceratids seem to have been influenced by episodic global climatic optimums.



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We express our sincere gratitude to R. A. Reymont (Swedish Museum of Natural History, Stockholm) and J. W. Haggart (Geological Survey of Canada, Vancouver) for critical reading of the manuscript. H. Hirano (Waseda University, Tokyo), S. Toshimitsu (Geological Survey of Japan, Tsukuba) and anonymous reviewers provided helpful suggestions and information. We are much indebted to K. Hasegawa (Mikasa) for providing the specimen, NSM PM16160. This study was financially supported by the Grant-in-Aid for JSPS Research Fellow (No. 6583 in 1998–1999) from the Ministry of Education, Science, Sports and Culture, Japan to F. Kawabe and by a grant from the Fujiwara Natural History Foundation (1999) to F. Kawabe and Y. Shigeta.

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## Some additional Wuchiapingian (Late Permian) ammonoids from the Southern Kitakami Massif, Northeast Japan

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**Abstract.** Permian ammonoids, *Dzhulfoceras* cf. *furnishi*, *D.* sp. and *Stacheoceras*? sp., are described from the Southern Kitakami Massif, Northeast Japan. The first two and the last were collected from the Lower and Middle Toyoman Series, respectively. The occurrence of *Dzhulfoceras* supports the previous correlation of the Lower Toyoman Series with the Wuchiapingian (Dzhulfian). This occurrence of *Dzhulfoceras* is the first record of the genus outside the Middle East and supports the conclusion that a close paleobiogeographic relationship existed between the Middle East and the Southern Kitakami in Late Permian time.

**Key words:** *Dzhulfoceras*, Equatorial Tethyan Province, Southern Kitakami Massif, *Stacheoceras*, Upper Permian, Wuchiapingian

### Introduction

Fossils including ammonoids are rare in the black shale of the Upper Permian Toyoman Series in the Southern Kitakami Massif, Northeast Japan. However, the few ammonoids that have been recovered are useful biostratigraphic tools for dating the Toyoman formations and for estimating the paleobiogeographic situation of the massif. To date, sixteen species belonging to 11 genera of ammonoids have been described from the Toyoman Series (Bando, 1975; Ehiro, 1996; Ehiro and Bando, 1985; Ehiro *et al.*, 1986; Murata and Bando, 1975). The genera are *Pseudogastrioceras*, *Stacheoceras*, *Timorites*, *Cyclolobus*, *Eumedicottia*, *Neogeoceras*, *Araxoceras*, *Vescotoceras*, *Eusanyangites*, *Xenodiscus* and *Paratirolites*. Based on these ammonoids, especially those belonging to the Cyclolobidae, Araxoceratidae, Xenodiscidae and Dzhulfitidae, the Lower to Middle and Upper Toyoman Series have been correlated with the Wuchiapingian (Dzhulfian) and Changhsingian (Dorashamian), respectively (Ehiro and Bando, 1985; Ehiro *et al.*, 1986; Ehiro, 1996). This ammonoid fauna is typical of the Equatorial Tethyan Province (Ehiro, 1997) and closely related to the Late Permian ammonoid faunas of South China and the Middle East.

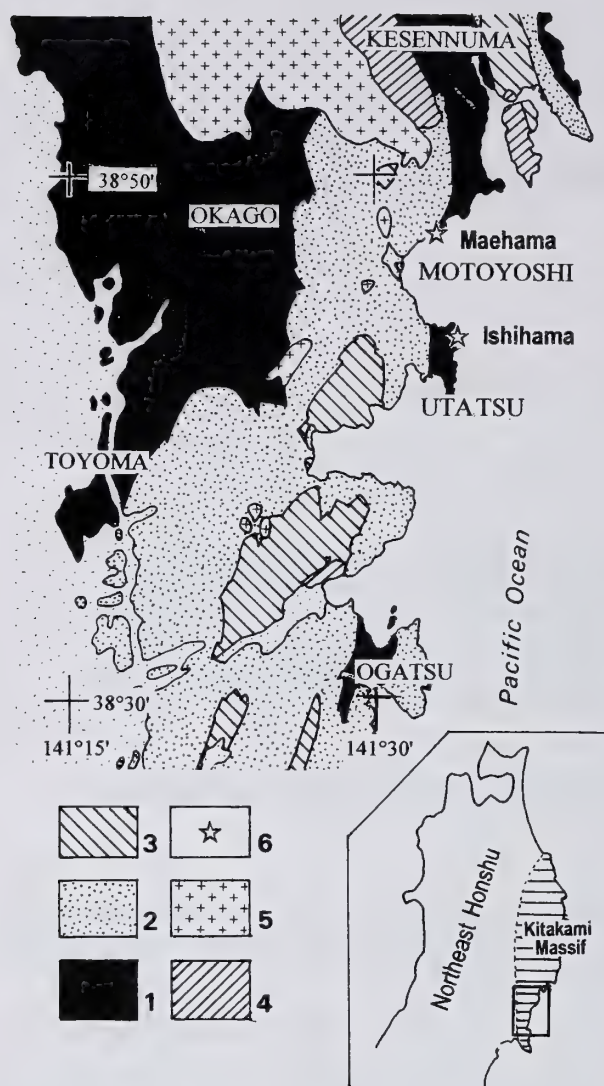
In this paper two new occurrences of Late Permian ammonoids are described. Two specimens were collected from the Suenosaki Formation in the Utatsu area, and one

specimen came from the Toyoma Formation in the Motoyoshi area (Figure 1). Both occurrences indicate the Wuchiapingian horizon.

### Late Permian ammonoids from Utatsu and Motoyoshi

In the Utatsu area, the uppermost Kanokuran (Middle Permian) to Middle Toyoman Suenosaki and Upper Toyoman Tanoura Formations are widely distributed (Ehiro and Bando, 1985). Two specimens of ammonoids described here as *Dzhulfoceras* cf. *furnishi* Ruzhencev and *D.* sp. were found in a calcareous nodule collected from a shale bed exposed along the Ishihama coast (see locality 3 of Ehiro and Bando, 1985). The fossil horizon belongs to the lower part of the Suenosaki Formation, which is correlated with the lower part of the Lower Toyoman Series. From this locality Ehiro and Bando (1985) and Ehiro *et al.* (1986) described some Wuchiapingian ammonoids, such as *Pseudogastrioceras* sp., *Stacheoceras iwaizakiense* Mabuti, *Timorites intermedius* (Wanner), *Araxoceras* cf. *rotoides* Ruzhencev, A. sp., *Vescotoceras japonicum* (Bando and Ehiro) and V. sp., and correlated the lower part of the Suenosaki Formation with the Wuchiapingian (Dzhulfian).

*Dzhulfoceras* belongs to the family Araxoceratidae and is indicative of Wuchiapingian age, although the genus ranges up to the Changhsingian. To date, three species of *Dzhulfoceras* have been described from the Upper Dzhulfian (*Vedioceras* bed) in Transcaucasia (*D. furnishi* Ruzhencev,



**Figure 1.** Map showing the fossil localities and geology of the southern part of the Southern Kitakami Massif. 1. Permian, 2. Triassic, 3. Jurassic, 4. Lower Cretaceous, 5. Early Cretaceous granitic rocks, 6. ammonoid localities.

*D. inflatum* Ruzhencev and *D. paulum* Ruzhencev; Ruzhencev, 1962, 1963) and from the Dorashamian (Unit 7 of the Hambast Formation) in Abadeh, Central Iran (*D. furnishi*; Bando, 1979). The Ishihama specimens of *Dzhulfoceras* described herein are the first recovery of the genus outside the Middle East. The *Dzhulfoceras* specimens show a close faunal relationship, in association with the previously reported ammonoids, to those of the Dzhulfian. The presence of *Dzhulfoceras* in South Kitakami supports the conclusion that the lower Suenosaki Formation is correlatable with the Wuchiapingian (Dzhulfian) (Ehiro and Bando, 1985), and that the South Kitakami region belonged to the Equatorial Tethyan ammonoid province during Permian time (Ehiro, 1997).

At the Maehama coast of the Motoyoshi area the Toyoma Formation consists mainly of massive black shale with a subordinate amount of lenticular thin sandstone beds. It is overlain unconformably by the Lower Triassic Hiraiso Formation. Murata and Bando (1975) reported an araxoceratid ammonoid, *Araxoceras* cf. *kiangsiense* Chao, from the black shale about 15 m below the boundary between the Toyoma and Hiraiso Formations. They correlated this part of the stratigraphic succession, which belongs to the Middle Toyoman Series based on the associated molluscan fossils, with the Dzhulfian. Later Zakharov (1986) compared this species to *Eusanyangites bandoi* Zakharov and Pavlov, which was recovered from the Wuchiapingian bed of Primorye, Far East Russia (Zakharov and Pavlov, 1986).

The present ammonoid specimen described here as *Stacheoceras*? sp. was collected from black shale exposed on the Maehama coast, at the same locality as Murata and Bando (1975). *Stacheoceras* is a long-ranging Permian genus and provides less precision in stratigraphic correlations.

### Systematic descriptions

Superfamily Cycloloboidea Zittel, 1895  
Family Vidrioceratidae Plummer and Scot, 1937  
Genus *Stacheoceras* Gemmellaro, 1887

*Type species.*—*Stacheoceras mediterraneum* Gemmellaro, 1887.

### *Stacheoceras*? sp.

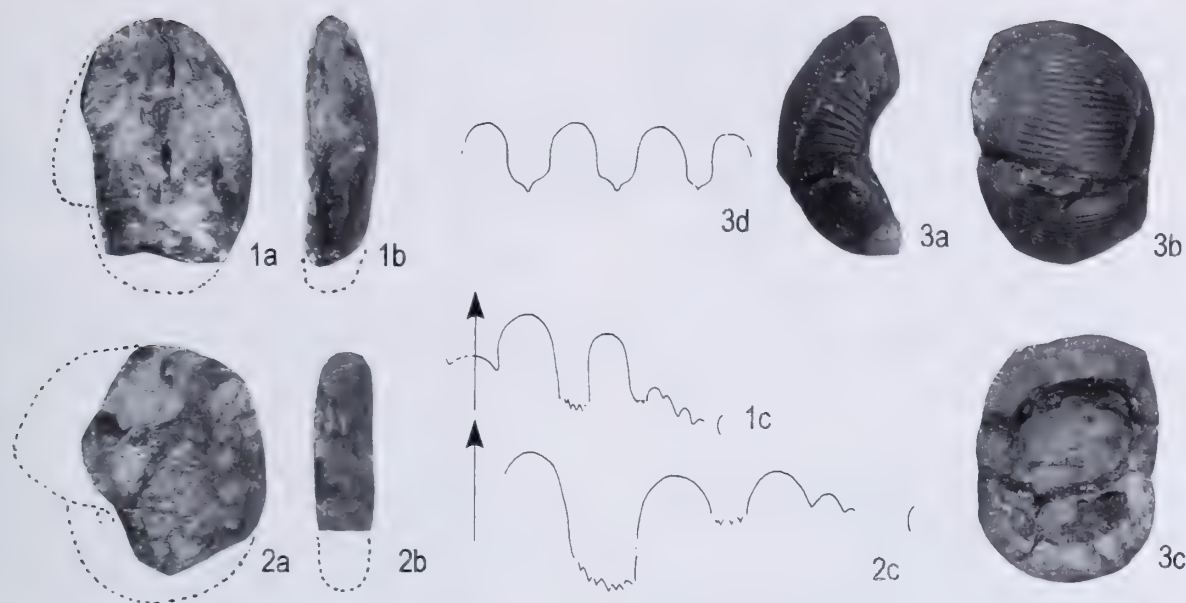
Figure 2.3a–d

*Material.*—A relatively small incomplete specimen, IGPS coll. cat. no. 108551, collected from the Toyoma Formation exposed on the Maehama coast, Motoyoshi-cho, Motoyoshigun, Miyagi Prefecture.

*Remarks.*—The specimen consists of about one half volution of the body chamber and fragments of phragmocone with an estimated diameter of 21 mm. The involute conch with a narrow umbilicus is subglobular (Figure 2.3a–c). At the maximum estimated diameter the height, width and umbilical diameter are about 12.0, 15.5 and 5.0 mm, respectively. The surface of the body chamber bears fine but prominent transverse ribs with intercalary ones, which start at 1/3 height of the whorl. The body chamber is also marked by rather prominent transverse constrictions, which are nearly straight. The suture lines, only partly preserved and displaying parts of the lateral suture, consist of more than three pairs of rounded saddles and trifid lobes (Figure 2.3d). Their exact positions with respect to the venter are unknown, because they are on a fragmental phragmocone.

Involute subglobular shells with transverse ribs are characteristic for some genera which belong to the families including and not limited to the Marathonitidae, Perrinitidae, Vidrioceratidae and Cyclolobidae. Judging from the shape of the trifid lateral lobe of the suture, it could belong to *Waagenia* or more likely *Stacheoceras*. The present speci-





**Figure 2.** 1. *Dzhulfoceras* cf. *furnishi* Ruzhencev, IGPS coll. cat. no. 108552, lateral (1a) and ventral (1b) views,  $\times 2.5$ , and suture line (1c),  $\times 7$ . 2. *Dzhulfoceras* sp., IGPS coll. cat. no. 108553, lateral (2a) and ventral (2b) views,  $\times 2.5$ , and suture line (2c),  $\times 7$ . 3. *Stacheoceras?* sp., IGPS coll. cat. no. 108551, lateral (3a), ventral (3b) and dorsal (3c) views,  $\times 1.6$ , and a part of the lateral suture line,  $\times 8$ . Dotted lines show estimated conch outlines.

men is, however, too poorly preserved to identify it with confidence at the generic level and therefore the specimen is placed in *Stacheoceras* with strong reservations.

Superfamily Otoceratoidea Hyatt, 1900  
Family Araxoceratidae Ruzhencev, 1959  
Genus *Dzhulfoceras* Ruzhencev, 1962

*Type species.*—*Dzhulfoceras furnishi* Ruzhencev, 1962.

*Dzhulfoceras* cf. *furnishi* Ruzhencev, 1962

Figure 2.1a–c

*Compare.*—

*Dzhulfoceras furnishi* Ruzhencev, 1962, p. 99, pl. 5, figs. 1a, b, text-fig. 8a; Bando, 1979, p. 128, pl. 6, figs. 8a–c, 9a, b, text-fig. 6A.

*Material.*—A partly complete phragmocone, IGPS coll. cat. no. 108552, collected from the lower part of the Suenosaki Formation exposed along the Ishihama coast, Utatsu-cho, Motoyoshi-gun, Miyagi Prefecture.

*Descriptive remarks.*—The specimen is a deformed phragmocone with an estimated diameter of 14 mm. The conch is involute and thinly discoidal, with a pinpoint umbilicus (Figure 2.1a, b). The compressed shell has nearly parallel, but slightly convex flanks. The venter and ventrolateral shoulders are rounded. No ornamentation is observed on the shell surface. The ceratitic suture consists of a moderately wide ventral lobe, large and high rounded ventrolateral saddle, large and deep first lateral lobe, moderately high second lateral saddle, relatively small and shallow

second lateral lobe and four pairs of small rounded saddles and pointed lobes (Figure 2.1c). Only the first and second lateral lobes are denticulate.

Based on the shell form, especially on the rounded shape of its ventrolateral part, and the form of the suture, the present specimen can be assigned with confidence to *Dzhulfoceras*. Among the species of the genus *Dzhulfoceras* it most closely resembles *D. furnishi* Ruzhencev in having nearly parallel sides of the shell. The present specimen is not sufficiently well preserved to allow a confident species assignment.

*Dzhulfoceras* sp.

Figure 2.2a–c

*Material.*—An incomplete phragmocone, IGPS coll. cat. no. 108553, collected from the lower part of the Suenosaki Formation exposed on the Ishihama coast, Utatsu-cho, Motoyoshi-gun, Miyagi Prefecture.

*Remarks.*—The specimen is a small fragment of phragmocone of about one half volution with an estimated diameter of 14 mm. The conch is compressed, involute and thinly discoidal. The slightly convex sides are subparallel, and the venter and the ventral shoulders are rounded (Figure 2.2a, b). No ornamentation is observed on the shell surface. The suture line is partly preserved on the lateral part of the conch. It consists of a large and high rounded ventrolateral saddle, large and deep serrated first lateral lobe, moderately high rounded second lateral saddle, relatively small and shallow serrated second lateral lobe and more than two pairs of small rounded saddles and pointed

lobes (Figure 2.2c). The ventral suture is not preserved.

This specimen is assigned to *Dzhulfoceras*, judging from the shell shape and sutural outline. It is, however, impossible to assign the specimen to a species with confidence because of the poor state of preservation.

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## Middle Carboniferous orthoconic cephalopods from the Omi Limestone Group, Central Japan

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**Abstract.** A Middle Carboniferous (probable late Bashkirian) fauna of orthoconic cephalopods was collected from bioclastic rudstone/grainstone in the Omi Limestone Group, Central Japan. This fauna belongs to the Taishaku-Akiyoshi-South China Faunal Province. Recognized herein are the orthocerid nautiloid *Bogoslovskya omiensis* sp. nov., the bactritids *Bactrites nagatoensis* Niko, Nishida and Kyuma, 1991 and *Bactrites* sp., and an indeterminate body chamber. This is the first reliable documentation of orthoconic cephalopods from the Omi Limestone Group.

**Key words:** Bactritida, Middle Carboniferous, Omi Limestone Group, Orthocerida

### Introduction

Since the beginning of the Twentieth Century, some Carboniferous cephalopods have been occasionally reported by non-specialists of this group from the Omi Limestone Group, an accreted reefal buildup in Niigata Prefecture, Central Japan. The taxa cited include *Gastrioceras* sp. by Yabe (1904), *Eoasianites* cf. *orientale* (Yin) by Kato and Nakamura (1962), *Eoasianites* sp., *Gastrioceras* aff. *reticulatus* Yin, *Paralegoceras* sp. and *Reticuloceras*? sp. by Igo and Koike (1963, 1964), *Pseudorthoceras* sp. by Koizumi (1975), and *Pseudoparalegoceras*? sp. and *Stroboceras* sp. by Oyagi (2000). Unfortunately, these taxa were presented without detailed descriptions and/or illustrations, so an evaluation of their significance can not be made at this time. As the first attempt to give a reliable documentation of the Omi cephalopod fauna, the present report sheds light on the orthoconic nautiloids and bactritoids for taxonomic, biostratigraphic and paleobiogeographic purposes.

The collecting site that yielded these cephalopods is situated at the southern corner of Higashiyama Quarry, Latitude 36°59'27"N and Longitude 137°47'8"E, where light gray, massive bioclastic rudstone/grainstone limestone is exposed. This cephalopod-bearing limestone is Middle Carboniferous (probable late Bashkirian) in age and may be part of the reef front facies (Niko and Hasegawa, 2000). The geologic setting of the Omi Limestone Group has been described in Hasegawa *et al.* (1969, 1982), Hasegawa and Goto (1990), and Nakazawa (1997), thus it will not be repeated herein. During field work in 1997 to 1999, nearly thirty specimens identified as *Bogoslovskya omiensis* sp.

nov., *Bactrites nagatoensis* Niko, Nishida and Kyuma, *Bactrites* sp., along with an indeterminate body chamber were collected in cooperation with Mr. Toshiaki Kamiya. This association of genera is characteristic of the Taishaku-Akiyoshi-South China Province (Niko, 2000).

All specimens studied are deposited in the University Museum of the University of Tokyo (UMUT).

### Systematic paleontology

Subclass Nautiloidea Agassiz, 1847

Order Orthocerida Kuhn, 1940

Superfamily Orthoceratoidea M'Coy, 1844

Family Orthoceratidae M'Coy, 1844

Subfamily Michelinoceratinae Flower, 1945

Genus *Bogoslovskya* Zhuravleva, 1978

*Type species.* — *Bogoslovskya perspicua* Zhuravleva, 1978.

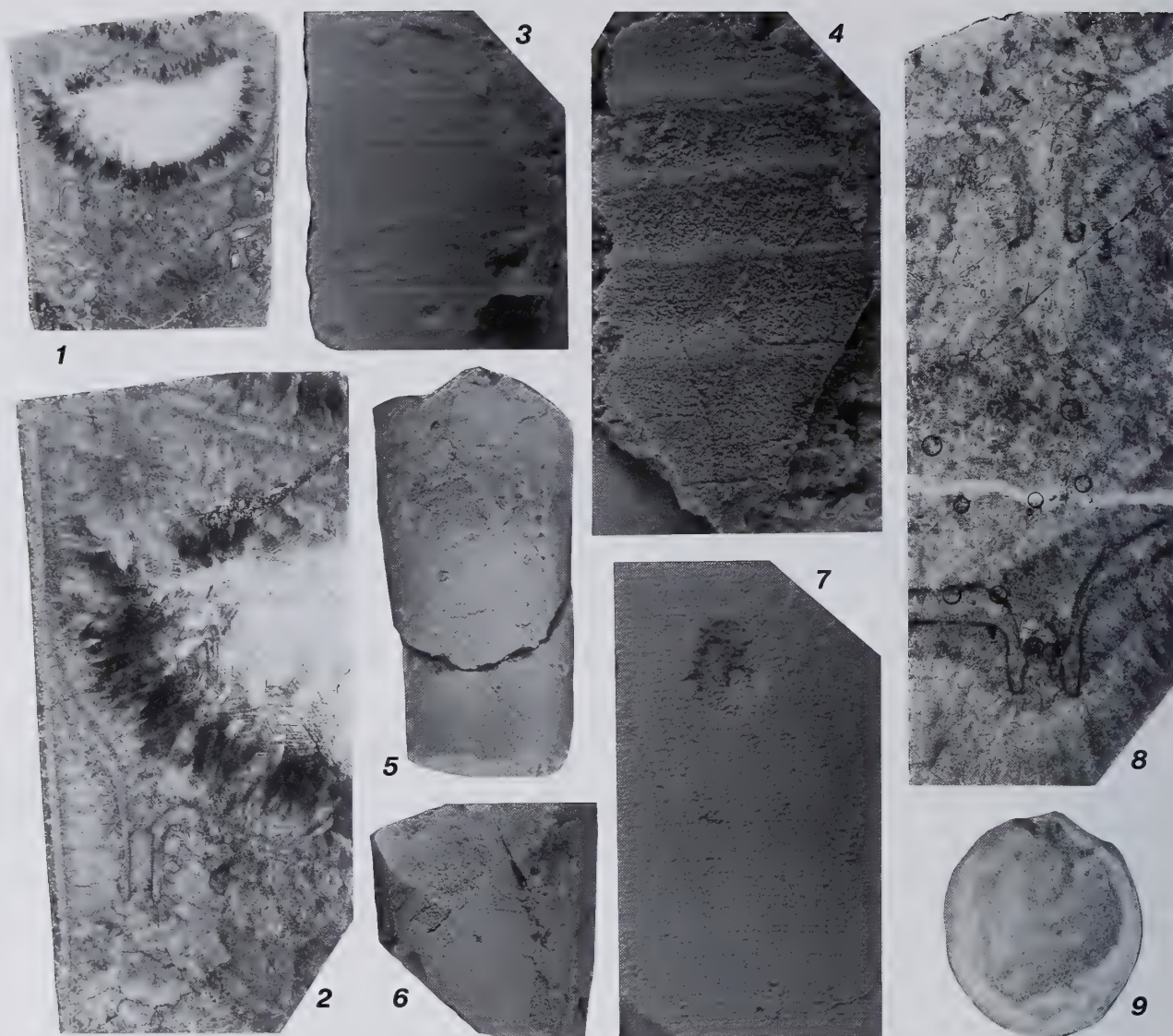
### *Bogoslovskya omiensis* sp. nov.

Figure 1.1–1.3, 1.5–1.9

*Diagnosis.*—Species of *Bogoslovskya* with 6°–7° angle of shell expansion, approximately 0.9 in form ratio of shell, transverse surface lirae; form ratio of camera 1.8–3.1; siphuncle strongly eccentric, its position ratio 0.13.

*Description.*—Orthocones with 6°–7° angle of shell expansion and laterally compressed cross section yielding lateral/dorsoventral diameter ratio (form ratio of shell) of approximately 0.9; largest specimen (paratype, UMUT PM 27892) of phragmocone reaches 16.5 mm in dorsoventral di-





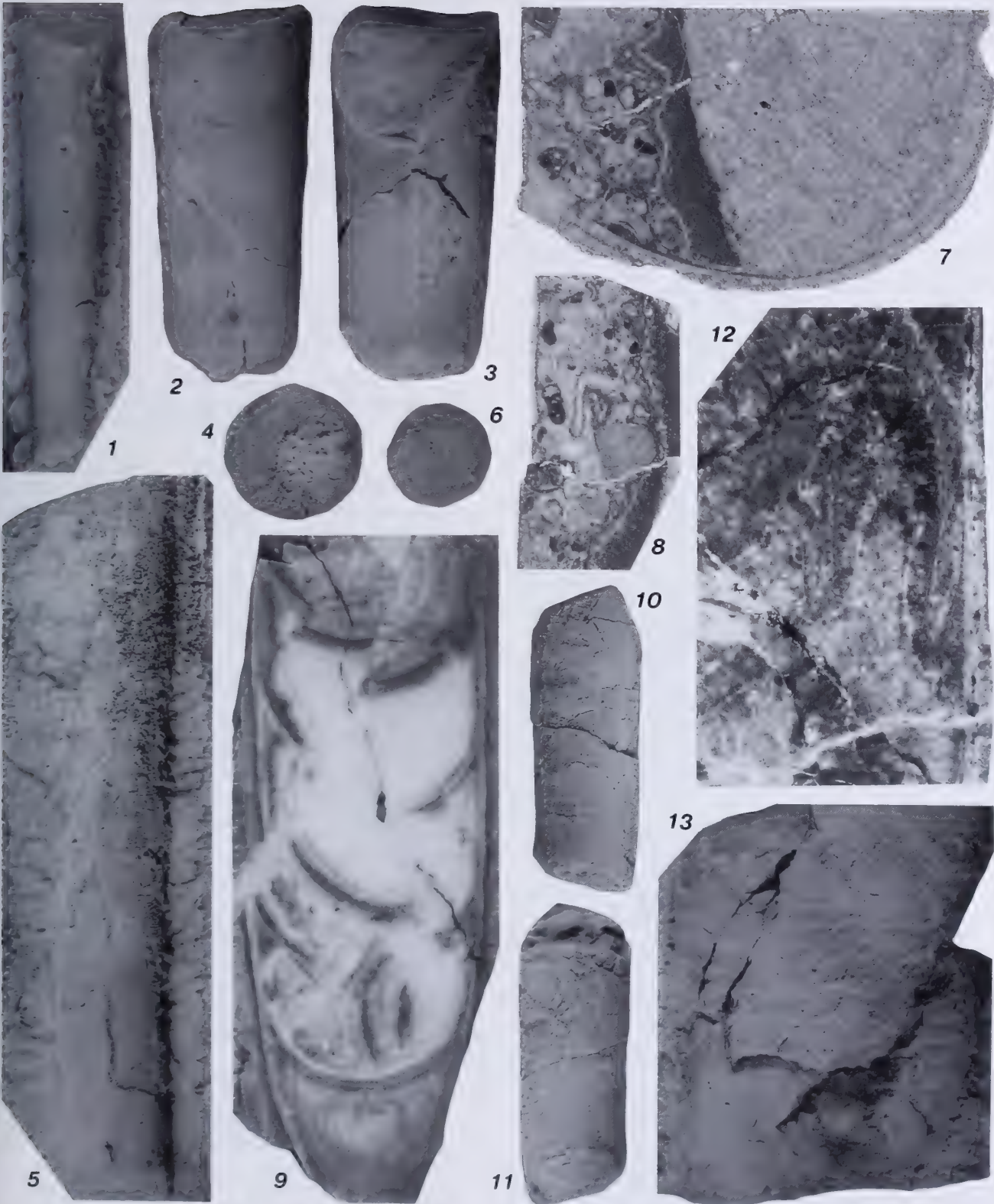
**Figure 1.** 1–3, 5–9. *Bogoslovskya omiensis* sp. nov. 1–3. Holotype, UMUT PM 27890; 1, dorsoventral thin section,  $\times 5$ ; 2, details of apical siphuncle,  $\times 14$ ; 3, details of surface ornamentation of apical shell,  $\times 10$ . 5, 8. Paratype, UMUT PM 27891; 5, side view of anti-siphuncular side,  $\times 2$ ; 8, details of adoral siphuncle, thin longitudinal (but not dorsoventral) section,  $\times 14$ . 6, 7, 9. Paratype, UMUT PM 27892; 6, side view, siphuncular side on right(?),  $\times 2$ ; 7, details of surface ornamentation of adoral shell,  $\times 10$ ; 9, polished section near adoral end, siphuncular side down(?), slightly deformed,  $\times 2$ . 4. Indeterminate body chamber, UMUT PM 27918, details of surface ornamentation,  $\times 5$ .

ameter. Surface ornamentation of apical shell (represented by holotype, up to 7.9 mm in dorsoventral diameter) consists of subdued transverse lirae with somewhat unequal size and intervals, then it shifts to closely spaced, fine, transverse

lirae on adoral shell (ditto paratypes). Sutures not observed, but obvious obliquity not observed in dorsoventral section. Septa moderately deep; cameral length relatively short for genus, 4.1 mm in length, with maximum dorsoventral diame-

→ **Figure 2.** 1–5. *Bactrites nagatoensis* Niko, Nishida and Kyuma, 1991. 1. UMUT PM 27897, dorsal view,  $\times 3$ . 2–4. UMUT PM 27895; 2, ventral view,  $\times 3$ ; 3, dorsal view,  $\times 3$ ; 4, apical view, venter down,  $\times 3$ . 5. UMUT PM 27896, dorsal view,  $\times 1.5$ . 6–12. *Bactrites* sp. 6–8, 10, 11. UMUT PM 27916; 6, apical view, venter down,  $\times 3$ ; 7, dorsoventral thin section, venter on left,  $\times 14$ ; 8, details of apical septal neck, venter on left,  $\times 14$ ; 10, ventral view,  $\times 3$ ; 11, dorsal view,  $\times 3$ . 9, 12. UMUT PM 27917; 9, longitudinal (near dorsoventral) polished section, venter on right,  $\times 2$ ; 12, details of adoral septal neck, longitudinal (near dorsoventral) thin section, venter on right,  $\times 14$ . 13. Indeterminate body chamber, UMUT PM 27918, side view,  $\times 1.5$ .







ter/length ratio (form ratio of camera) 1.8 in apical shell; this ratio increases to 2.5–3.1 in adoral shell. Siphuncular position strongly eccentric and submarginal, minimum distance of central axis of siphuncle from shell surface per corresponding dorsoventral shell diameter (siphuncular position ratio) is 0.13 in holotype. Septal necks long for family; they are orthochoanitic and cylindrical in apical shell, then shifts gently tapering and funnel-shaped orthochoanitic forms in adoral shell; length of septal necks on anti-siphuncular (dorsal?) side ranges from 1.03 mm to 1.28 mm; siphuncular diameters 0.42–0.70 mm at tips of septal neck, where septal foramen is 0.23–0.42 mm in diameter, giving a diameter of septal neck/corresponding dorsoventral shell diameter ratio of approximately 0.06. Annulus of weak auxiliary deposits recognized in septal foramina. Connecting ring not preserved; no cameral deposits detected.

**Discussion.**—Among the three previously known Upper Paleozoic species of this genus (see Niko *et al.*, 1995, 1997, Niko and Ozawa, 1997), *Bogoslovskya omiensis* sp. nov. bears the greatest similarity to *B. akiyoshiensis* Niko, Nishida and Kyuma (1995, figs. 1.1–1.14) from the Middle Carboniferous (Moscovian) in the Akiyoshi Limestone, Southwest Japan. Although the gross shell shape and the surface ornamentation suggest the close phylogenetic relationship of the both species, the main character of *Bogoslovskya omiensis* that separates it from *B. akiyoshiensis* is the more eccentric siphuncular position, with a siphuncular position ratio of 0.13 versus 0.19 for the corresponding shell diameter in *B. akiyoshiensis*.

**Etymology.**—The specific name is derived from the Omi Limestone Group, in which this species occurs.

**Material examined.**—The holotype, UMUT PM 27890, is an incomplete phragmocone 9.3 mm in length. The following two paratypes of the incomplete phragmocones are assigned: UMUT PM 27891, 27.0 mm in length, and UMUT PM 27892, 12.8 mm in length. They represent more adoral shells than the holotype. In addition, two fragmentary specimens, UMUT PM 27893, 27895 are referred to this species with reservation.

Subclass Bactritoidea Shimanskiy, 1951

Order Bactritida Shimanskiy, 1951

Family Bactritidae Hyatt, 1884

Genus *Bactrites* Sandberger, 1843

**Type species.**—*Bactrites subconicus* Sandberger, 1843.

***Bactrites nagatoensis*** Niko, Nishida and Kyuma, 1991

Figure 2.1–2.5

*Bactrites nagatoensis* Niko, Nishida and Kyuma, 1991, p. 715, figs. 2.1–2.10, 3.1–3.5.

*Bactrites* cf. *nagatoensis* Niko, Nishida and Kyuma. Niko *et al.*, 1997, p. 106, figs. 3.9, 4.8.

**Discussion.**—Twenty-one bactritid specimens of the orthoconic phragmocones with an angle of adoral shell expansion of approximately 5°–6° were collected from Higashiyama Quarry. The shell diameters range from 2.3 mm (UMUT PM 27907) to 25.1 mm (UMUT PM 27915).

They have the shell morphology typical of the holotype, which is from the Moscovian (Middle Carboniferous) of the Akiyoshi Limestone, with rapid shell expansion for *Bactrites* and a single dorsal carina throughout the known phragmocone. A form possibly conspecific with this species also occurs in the Moscovian limestone of the Dala (Huanglong) Formation, Guizhou Province, South China (Niko *et al.*, 1997). Comparisons of *Bactrites nagatoensis* to three Laurentian species (*B. finisensis* Mapes, 1979, pl. 23, figs. 4–6, *B. mexicanus* Miller, 1944, pl. 20, figs. 8, 9, pl. 21, figs. 4–6, and *B. peytonensis* Mapes, 1979, pl. 8, figs. 4–14, pl. 9, figs. 2, 3, 6–8, 12, 13, 15, 17–19, pl. 14, figs. 7, 8, 10) having a dorsal carina are referable in Niko *et al.* (1991, p. 715).

**Material examined.**—UMUT PM 27895–27915.

### *Bactrites* sp.

Figure 2.6–2.12

**Description.**—Orthocones with gradual shell expansion indicating near 2° in angle; cross section of shell circular; largest specimen (UMUT PM 27917) attains approximately 19 mm (slightly deformed) in diameter at adoral phragmocone. Surface ornamentation and carina absent, wrinkled layer not observed. Except for ventral lobe, sutures are nearly straight and slightly oblique at 6°–15° to rectangular direction of shell axis, toward aperture on dorsum. Septal curvature moderate; cameral length moderate with approximately 1.6 in diameter/length ratio. Siphuncular position ventral margin; ventral septa attached to shell wall; septal necks orthochoanitic, relatively long for genus; dorsal septal necks 0.82–1.26 mm in length; diameter of septal foramen/corresponding shell diameter is approximately 0.07; connecting ring not preserved. No cameral and endosiphuncular deposits detected.

**Discussion.**—This species is known from the two fragmentary phragmocones, but is easily separable from associated *Bactrites nagatoensis* by the slenderer shell and the lacking a dorsal carina. The features approach those of *Bactrites carbonarius* Smith (1903, pl. 6, figs. 9–11), *B. fayettevillensis* Mapes (1979, pl. 9, figs. 9–11, pl. 10, figs. 6–8, pl. 13, figs. 1, 7, 8, 11, 12, 14–16, pl. 14, fig. 9, pl. 15, figs. 1, 2, 6, 7, 12–14), *B. longocameratus* Shimanskiy (1949, fig. 1), *B. milleri* Mapes (1979, pl. 10, fig. 10, pl. 12, figs. 4, 8–12), *B. quadrilineatus* Girty (1909, pl. 6, figs. 1, 1a, 1b, 2–4, 4a), *B. smithianus* Girty (1909, pl. 6, fig. 5, 6?), and *B. sp.* (Niko *et al.*, 1991, figs. 3.6–3.9). Due to the poor preservation of the Omi specimens and the relatively simple morphology of this group for *Bactrites*, specific comparisons cannot be made at this time.

**Material examined.**—UMUT PM 27916, 27917.

Subclass, Order, Superfamily, Family, Genus,  
and Species uncertain

body chamber

Figures 1.4, 2.13

**Discussion.**—A fragmentary body chamber of an orthoconic shell, 67.5 mm in length and 39 mm+ (deformed)



in diameter, is available for this study. Although its surface ornamentation consisting of weak annulations and lirae shows an affinity to the mature modification of some bactritids including *Bactrites peytonensis* Mapes and *Bactrites?* sp. morphotype 13 (Mapes, 1979, pl. 2, figs. 14–16), lack of knowledge of the siphuncular structure and position precludes a positive identification even to be subclass level. Similar ornamentation is also known to occur in the Carboniferous orthocerids, such as *Brachycycloceras* (Miller *et al.*, 1933), *Cryptocycloceras* (Shimansky, 1968), *Cycloceras* (M'Coy, 1844), and *Reticycloceras* (Gordon, 1960).

*Material examined*.—UMUT PM 27918.

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# Mode of occurrence and composition of bivalves of the Middle Jurassic Mitarai Formation, Tetori Group, Japan

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**Abstract.** The Middle Jurassic Mitarai Formation distributed in Shokawa Village, Gifu Prefecture, central Japan, is interpreted as deposits of wave-dominated shelf environments. The muddy shelf deposits yield abundant molluscs showing various modes of occurrence that can be divided into three fossil assemblages: (1) the autochthonous *Modiolus maedae*-*Tetorimya carinata* assemblage with commonly *in-situ* preserved semi-infauna and deep burrowers; (2) the *Entolium inequivalve* assemblage characterized by mixed autochthonous infauna and parautochthonous free-living elements; and (3) the allochthonous *Inoceramus maedae* assemblage. The *Entolium inequivalve* assemblage contains the chemosymbiotic bivalve *Solemya* and is associated with a low-diversity ichnofauna suggestive of low oxygen conditions.

**Key words:** bivalves, fossil assemblage, ichnofauna, Jurassic, low oxygen condition, Mitarai Formation, taphonomy

## Introduction

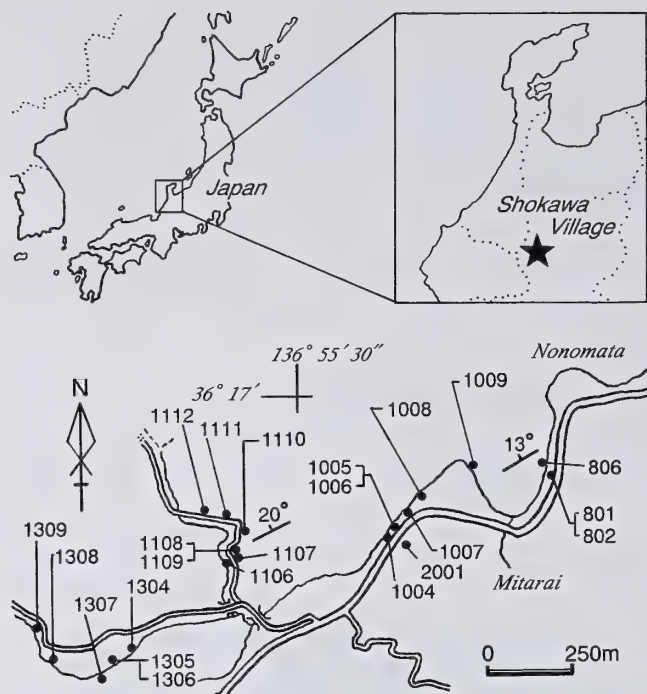
The Middle Jurassic Mitarai Formation, Tetori Group, is exposed in the vicinity of Shokawa Village, Gifu Prefecture, central Japan (Figure 1) and is composed of shallow marine deposits. The formation yields abundant benthic macrofossils and has been well studied by geologists and palaeontologists (Maeda, 1952, 1961; Hayami, 1959a, b, 1960; Masuda *et al.*, 1991; Matsukawa and Nakada, 1999). Maeda (1952) and Matsukawa and Nakada (1999) provided the geologic map and described the stratigraphy of the formation in this area. Masuda *et al.* (1991) broadly discussed the depositional environments and tectonic nature of the Tetori basin situated along the East Asian continental margin. The benthic fauna of the Mitarai Formation mainly consists of bivalves. It has been described from a taxonomic point of view by Hayami (1959a, b, 1960). However, no palaeoecological or taphonomic studies of this fauna exist, although the bivalves show variable modes of occurrence ranging from an apparently allochthonous type to an autochthonous type preserving the life orientation. Moreover, the relationship between depositional environments and benthic assemblages, faunal compositions and ichnofauna are hardly known in the Jurassic of East Asia.

In this paper, the depositional environments of the Mitarai Formation are reconstructed based on facies analysis. The bivalves are grouped into three fossil assemblages, and their habitats and the nature of the assemblages are discussed. Particular emphasis has been placed on the composition of the benthic fauna and the modes of fossil occurrences which are described in detail.

## Geological framework

The Jurassic to Cretaceous Tetori Group is composed of nonmarine and shallow-marine deposits, and is widely distributed in the north-central part of Japan (Figure 1). The group is divided into three subgroups, the Kuzuryu, Itoshiro and Akaiwa in ascending order (Maeda, 1952, 1961). The Kuzuryu Subgroup is subdivided into the Ushimaru and Mitarai formations (Matsukawa and Nakada, 1999). These formations typically crop out in the study area of the Shokawa Village, Gifu Prefecture.

The lower part of the Ushimaru Formation unconformably overlies basal granitic rocks, and consists of fluvial, coarse clastic deposits and estuarine (in a broad sense) deposits containing abundant brackish-water molluscs such as *Crassostrea* sp., *Myrene tetoriensis* and *Tetoria yokoyamai*.



**Figure 1.** Map of Shokawa Village, showing the localities of molluscan fossil samples from the Mitarai Formation.

The upper Ushimaru Formation is composed of alternating beds of sandstone and mudstone commonly yielding brackish-water and marine molluscs, and is interpreted as estuarine and shallow marine deposits, which are conformably overlain by the marine Mitarai Formation (Kumon and Kano, 1991; Matsukawa and Nakada, 1999). The Mitarai Formation is about 45 m thick and consists of a basal conglomerate, sandstone and dark grey mudstone with abundant marine fossils such as ammonites, crinoids, gastropods and bivalves (Figure 2). The ammonite, *Lilloetia* sp., suggests a Callovian (Middle Jurassic) age (Sato and Kanie, 1963). This formation is overlain by shallow marine sandstone of the Otaniyama Formation, Itoshiro Subgroup (Maeda, 1952; Kumon and Kano, 1991; Matsukawa and Nakada, 1999).

#### Lithostratigraphy and depositional environments of the Mitarai Formation

##### Lithostratigraphy

The succession ranging from the uppermost Ushimaru Formation to the Mitarai Formation yields abundant marine molluscan fossils and is characterized by a transgressive sequence followed by regression (Matsukawa and Nakada, 1999). The uppermost Ushimaru Formation is composed of conglomerate and sandstone (Figure 2). The Mitarai Formation is mainly dominated by mudstone. The uppermost Ushimaru Formation of this paper is almost equivalent to the M1 member of the Mitarai Formation (Hayami, 1959).

The uppermost part of the Ushimaru Formation is composed of about 16 m of thick fine-grained sandstone with an

about 40-cm-thick basal conglomerate bed. This conglomerate bed contains well rounded pebbles and cobbles, and exhibits a sharp erosional contact with the underlying sandstone. The sandstone is characterized by hummocky cross-stratification and bioturbation. Maeda (1952) and Hayami (1960) reported the marine bivalve *Inoceramus maedae* from this sandstone. The HCS sandstone is capped locally by a thin conglomerate, which marks the base of the Mitarai Formation. The lower part of the Mitarai Formation consists of mudstone interbedded with trough and hummocky cross-stratified and parallel-laminated sandstone beds. The alternating beds of mudstone and sandstone gradually change upward into bioturbated massive mudstone. The upper part of this mudstone is intercalated with thin, parallel-laminated sandstone beds (1–4 cm thick) and a thick, very fine-grained sandstone bed (Loc. 1112). It is finally overlain by fine- to medium-grained sandstone of the Otaniyama Formation. The sandstone of the basal Otaniyama Formation yields rare disarticulated valves and fragments of *Inoceramus maedae*. The upper Mitarai Formation and the basal Otaniyama Formation form a coarsening-upward succession.

##### Depositional environments

The HCS sandstone of the upper Ushimaru Formation containing typical shallow marine bivalves is interpreted as wave-dominated nearshore sediments deposited above fair-weather wave base. HCS is a diagnostic sedimentary structure formed under waning storm and wave or combined-flow conditions (e.g. Duke *et al.*, 1991; Cheel and Leckie, 1993). HCS sandstones without associating muddy sediments imply deposition shallower than fair-weather wave base (Walker and Plint, 1992). The conglomerate bed at the base of the HCS sandstone (Figure 3.1) is in erosional contact with estuarine deposits of the Ushimaru Formation. This erosional surface, probably a result of strong shoreface erosion during transgression, marks an increase in water depth. Thus, the conglomerate can be interpreted as a transgressive lag deposit.

The Mitarai Formation is composed mainly of mudstone yielding marine fossils, which is interpreted to represent inner and outer shelf deposits below fair-weather wave base. In the lower part, the alternating beds of HCS sandstone and bioturbated mudstone probably indicate deposition during repetition of storm and fair-weather conditions in inner shelf environments. Parallel-laminated sandstone beds possibly represent tempestites generated by storm-induced flow (Walker and Plint, 1992). Bioturbated thick mudstone without sandstone intercalation overlying these alternating units may reflect an increase in water depth during transgression, and is interpreted as outer shelf deposits.

The thick sandstone beds of the upper Mitarai Formation (Locs. 1308, 1112) and the basal sandstone of the Otaniyama Formation (Loc. 1309) contain *Inoceramus maedae*, and probably represent nearshore environments. The coarsening- and shallowing-upward successions of the upper Mitarai and basal Otaniyama formations are interpreted to indicate deltaic systems (Kumon and Kano, 1991; Matsukawa and Ito, 1995), suggesting a regressional phase, that is, relative sea-level fall.



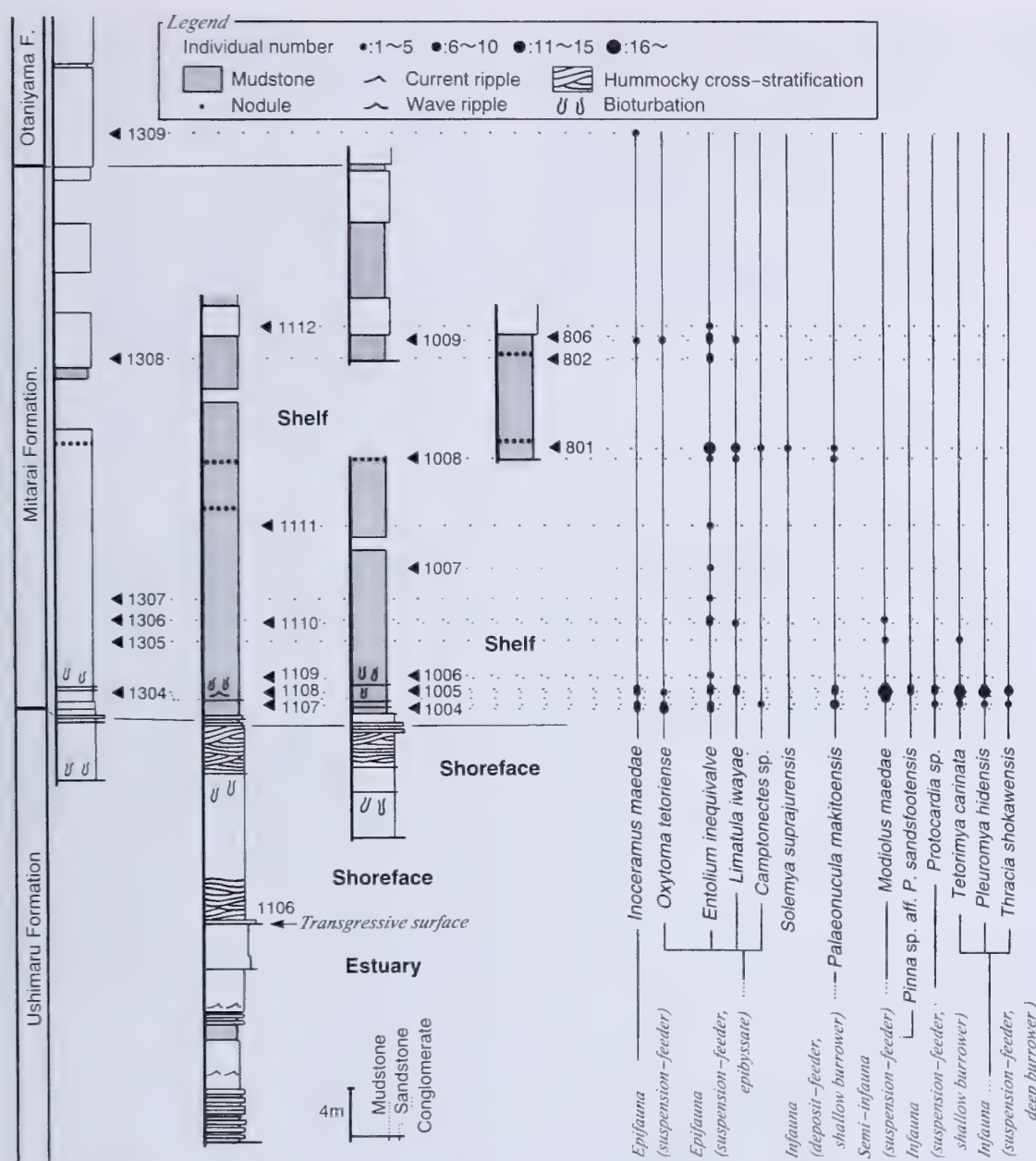


Figure 2. Columnar sections of Mitarai and Otaniyama Formations, showing the horizons of the samples examined and stratigraphic occurrences of bivalve species.

### Mode of occurrence and composition of bivalves

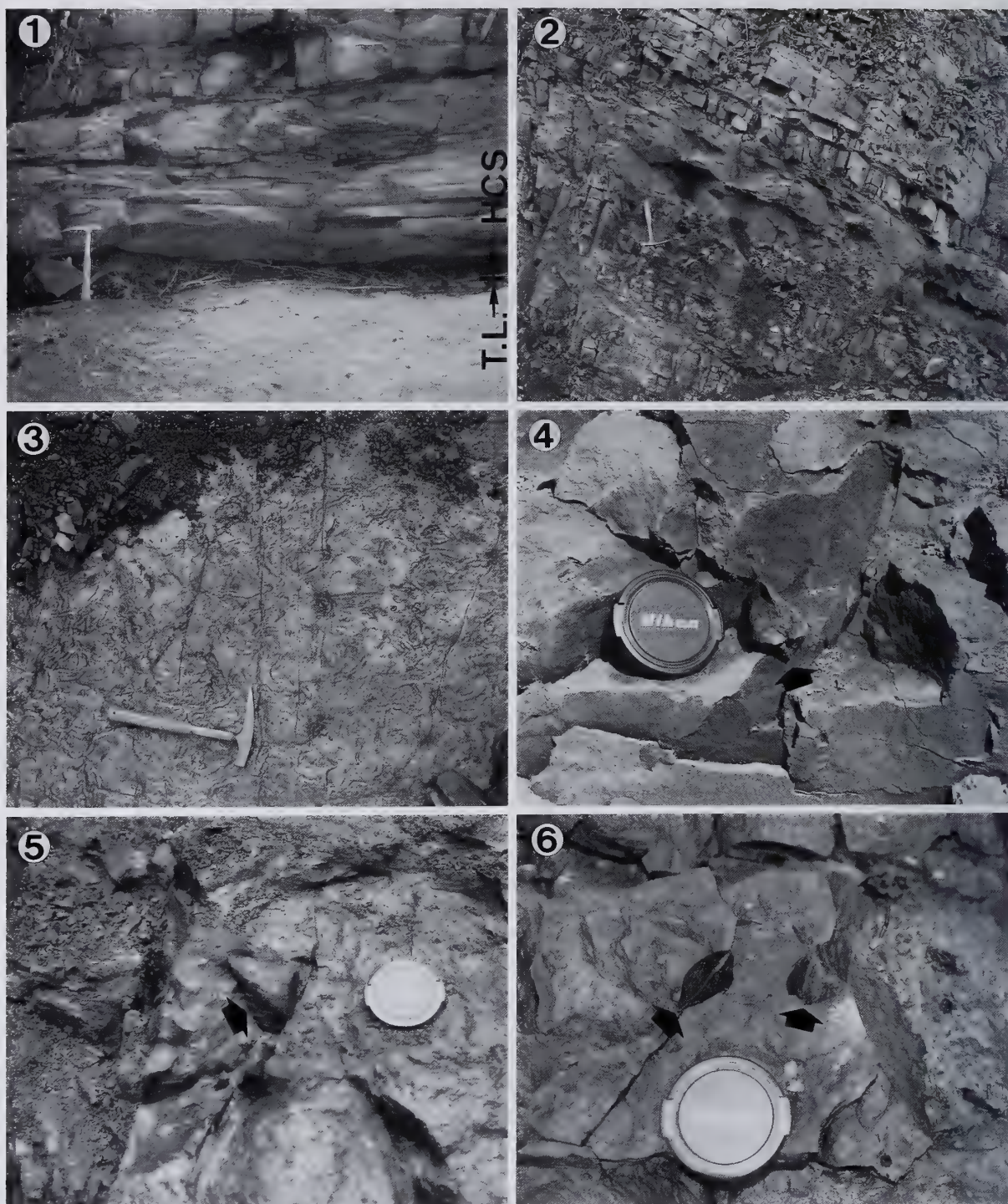
#### Methods

Bivalve fossils are found very sporadically in muddy deposits of the Mitarai Formation. These shells do not form shell beds, except for minor shell lenses in several horizons. Bivalves were counted on outcrop surfaces, and were collected bed by bed. Due to the limited material and marked differences in fossil preservation between samples, we did not carry out quantitative analysis of the fossil assemblages.

Based on the faunal composition and modes of fossil occurrences the samples from various localities were grouped in three assemblages, the *Modiolus maedae*-*Totorimya carinata*, the *Entolium inequivalve*, and the *Inoceramus maedae* assemblage. The *Inoceramus maedae* assemblage, which exceptionally forms minor shell lenses, was distinguished from the others by its mode of occurrence.

Life habits of the bivalves were reconstructed based on analogy with closely related living taxa, and also by referring to previous studies (Scott, 1974; Wright 1974; Fürsich, 1977,





**Figure 3.** Photos showing sedimentary structures, trace fossils and modes of fossil occurrences. **1.** Conglomerate and overlying hummocky cross-stratified sandstone (HCS) (Ushimaru Formation, loc. 1106). The conglomerate is interpreted to represent a transgressive lag deposit (T.L.). The hammer is 28 cm long. **2.** Exposure of alternating beds of sandstone and mudstone (lower Mitarai Formation, loc. 2001). **3.** Bedding plane of intensely bioturbated mudstone with large two-dimensional burrows (lower Mitarai Formation, loc. 1108). **4.** Vertical section of mudstone containing articulated *Tetorimyia carinata* Hayami (arrowed) (lower Mitarai Formation, loc. 1108). **5.** Vertical section of mudstone containing articulated *Modiolus maedae* Hayami (arrowed) (lower Mitarai Formation, loc. 1108). **6.** Plan view of mudstone containing articulated *Modiolus maedae* Hayami (arrowed) (lower Mitarai Formation, loc. 1005). Posterior parts of *M. maedae* are found.



1984; Aberhan, 1994).

***Modiolus maedae-Tetorimyia carinata* assemblage**

This assemblage contains the following bivalves: the deep-infaunal *Tetorimyia carinata*, *Thracia shokawensis*, *Pleuromya hidensis*, and *Goniomyia* sp.; the endobyssate *Modiolus maedae* and *Pinna* sp. aff. *P. sandfootensis*; the shallow infaunal *Palaeonucula makitoensis*, "*Palaeoneilo*"

sp., and *Protocardia* sp.; and the epibyssate or free-living *Entolium inequivalve*, *Limatula iwayae*, *Oxytoma tetoriense*, *Chlamys mitaraiensis* and *Camptonectes* sp. (Figure 4).

*M. maedae* and *T. carinata* are characteristic species of this assemblage. The *M. maedae-T. carinata* assemblage consists of abundant deep-burrowers, two semi-infaunal taxa, and several shallow infaunal and epifaunal elements. The deep-burrowing, semi-infaunal and shallow infaunal bi-



**Figure 4.** Bivalves from the Mitarai Formation. All specimens  $\times 1.0$ . 1. *Modiolus maedae* Hayami. Left external cast, lower Mitarai Formation, loc. 1108. 2. *Tetorimyia carinata* Hayami. Left valve, lower Mitarai Formation, loc. 2001. 3. *Pleuromya hidensis* Hayami. Left external cast, lower Mitarai Formation, loc. 1108. 4. *Protocardia* sp. with gaping articulated valves (butterfly position), lower Mitarai Formation, loc. 1108. 5. *Entolium inequivalve* Hayami. Right valve, upper Mitarai Formation, loc. 801. 6. *Goniomyia* sp. Left external cast, lower Mitarai Formation, loc. 1108. 7. *Limatula iwayae* Hayami. Right external cast, upper Mitarai Formation, loc. 1008. 8. *Oxytoma tetoriense* Hayami. Left external cast, lower Mitarai Formation, loc. 1108. 9. *Thracia shokawensis* Hayami. Left external cast, lower Mitarai Formation, loc. 1108. 10. *Solemya suprajurensis* Hayami with gaping articulated valves (butterfly position), upper Mitarai Formation, loc. 801. 11. Fragment of *Inoceramus maedae* Hayami (external mould) and ammonite from shell lens, lower Mitarai Formation, loc. 1005.



valves occur usually dispersed and are almost invariably preserved as articulated valves. *M. maedae*, *T. carinata* and *P. hidensis* are arranged with their sagittal plane perpendicular to the bedding plane with their posterodorsal or posterior margin pointing upward (Figures 3.4–6, 5) which is interpreted as keeping their life orientation. Especially all 50 individuals of *M. maedae* collected during the study are articulated and preserved *in situ*. Shells of *Pinna* sp. also preserve their life position with the umbones directed downward. Some of the shallow infaunal bivalves such as *Palaeonucula makitoensis* and *Protocardia* sp. are found articulated in butterfly position. Epifauna is usually disarticulated, only rarely articulated. Occasionally, disarticulated epifaunal bivalves, fine shell debris and crinoid fragments form small shell lenticles (about 1 cm thick and 10–30 cm wide) with plant fragments. This assemblage occurs in bioturbated mudstone with intercalated thin sandstone beds in the lower part of the Mitarai Formation, which represents inner shelf deposits within the transgressive phase of the formation.

#### **Entolium inequivalve assemblage**

The assemblage consists of the shallow-burrowing *Palaeonucula makitoensis* and "*Palaeoneilo*" sp., the epifaunal *Entolium inequivalve* and *Limatula iwayae*, and the deep-infaunal *Solemya suprajurensis*.

The *E. inequivalve* assemblage is characterized by a mixture of epifaunal and shallow infaunal bivalves. *E. inequivalve* and *L. iwayae* are common and occasionally preserved parallel to the bedding plane. Although the epifauna is usually disarticulated, the right and left valve of the same individual occasionally overlap. Shallow infaunal burrowers consist of the deposit-feeding bivalves *P. makitoensis* and "*Palaeoneilo*" sp., and are usually preserved in articulated condition. The very rare *S. suprajurensis* is also preserved with their valves articulated. This assemblage is found in bioturbated mudstone of the upper Mitarai Formation, except in its lower part (Locs. 801, 806, 1008).

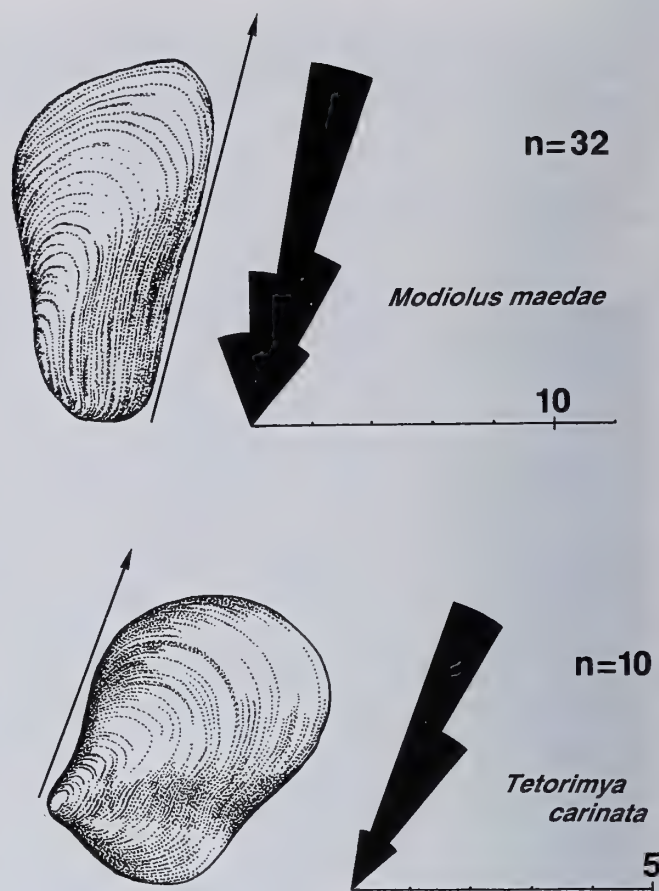
#### **Inoceramus maedae assemblage**

The assemblage is characterized by the co-occurrence of the epifaunal bivalves *Inoceramus maedae*, *Entolium inequivalve*, *Limatula iwayae*, and *Oxytoma tetoriense*, and the shallow-burrowing *Palaeonucula makitoensis* and *Protocardia* sp.

Epifauna dominates, in particular disarticulated and fragmented valves of *I. maedae*. *E. inequivalve*, *L. iwayae*, *O. tetoriense*, *P. makitoensis* and *Protocardia* sp. rarely occur in disarticulated and fragmented condition. These bivalves usually form small shell lenses (20–100 cm wide) associated with ammonites, crinoids, and abundant plant fragments. Some of the ammonites are fragmented and show selective dissolution of inner whorls. The shell lenses commonly overlie HCS and parallel-laminated sandstone beds. This assemblage is found throughout the Mitarai Formation (Locs. 1004, 1009).

#### **Trace fossils**

The lower part of Mitarai Formation (inner shelf deposits)



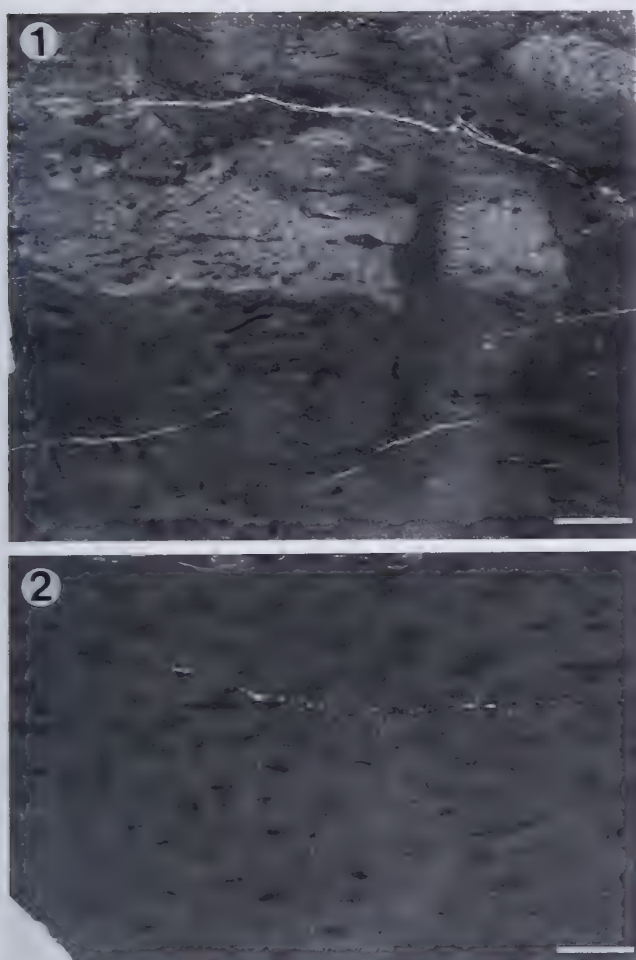
**Figure 5.** Modes of fossil occurrences of *Modiolus maedae* Hayami and *Tetorimyia carinata* Hayami. Almost all specimens are arranged with their sagittal plane perpendicular to the bedding plane with the posterodorsal or posterior margin pointing upward.

contains several kinds of trace fossils; *Spirophycus* isp., *Phycosiphon* isp., *Skolithos* isp., *Palaeophycus* isp., *Teredolites* isp., and a large two-dimensional burrow (*Beaconites*?; Figures 3.3, 6.1). *Skolithos* isp., *Palaeophycus* isp., the large two-dimensional burrows and intense obscure mottling are restricted to this horizon, whereas *Spirophycus* isp. and *Phycosiphon* isp. are very abundant throughout the Mitarai Formation.

The upper part of the Mitarai Formation, which can be interpreted to represent an outer shelf environment, is characterized by low diversity of trace fossils consisting solely of *Spirophycus* isp. and *Phycosiphon* isp. (Figure 6.2). Beds full of *Spirophycus* (15–70 cm thick) are common in this part.

*Teredolites* isp. is a boring in drift wood produced by wood-boring bivalves (Teredinidae). These wood pieces are commonly found within small shell lenses including *Inoceramus maedae* and ammonite fragments.





**Figure 6.** Vertical section of bioturbated mudstones of the lower Mitarai Formation: (1), loc. 1108, and the upper Mitarai Formation: (2), loc. 801. Scale bars are 1cm. 1. *Spirophycus* isp., *Skolithos* isp. and obscure mottling are found. 2. *Spirophycus* isp. Note low diversity of trace fossils.

## Discussion

### Autochthonous and allochthonous occurrence of bivalves

The *Modiolus maedae*-*Tetorimyia carinata* assemblage is composed mainly of autochthonous bivalves. Almost all deep infaunal and semi-infaunal bivalves are preserved with their sagittal plane perpendicular to the bedding, which is indicative of their life orientation (Figures 3.3-6, 5, 7). In particular, the modes of occurrence of *Modiolus* and *Pinna* are very similar to that of present-day ones. Shallow infaunal bivalves, such as *Palaeonucula* and *Protocardia*, are articulated and do not retain their life position, indicating that these taxa were easily exhumed after death. The members of this assemblage probably occur more or less *in situ*, and are interpreted as the autochthonous fauna of inner shelf deposits.

By contrast, the *Entolium inequivalve* assemblage is dominated by the epifaunal recliners *E. inequivalve* and *Limatula iwayae* and occurs in outer shelf deposits. Most examples of the two taxa are preserved with their valves disarticulated; rarely, disarticulated valves of the same individual overlap each other. Therefore, most epifaunal species are interpreted to represent parautochthonous occurrences. Articulated *Palaeonucula makitoensis* and *Solemya suprajurensis* probably indicate autochthonous occurrences.

Epifaunal elements of the *Inoceramus maedae* assemblage are considered to be typically allochthonous. *I. maedae* from muddy shelf deposits invariably is fragmented and disarticulated and occurs in shell lenses overlying storm sand sheets. *I. maedae* occurs in coastal sandstones of the basal Otaniyama Formation (Loc. 1309), as well as in the HCS sandstones of the Ushimaru Formation (Maeda, 1952; Hayami, 1960). Probably *I. maedae* underwent transport from nearshore areas during storm events.

### Influence of low oxygen conditions on the infauna of the *Entolium inequivalve* assemblage

The *Entolium inequivalve* assemblage, occurring in open shelf environments, is composed of an autochthonous infauna and a parautochthonous free-living epifauna. The infauna was probably influenced by low oxygen conditions. The assemblage is characterized by a low-diversity fauna and consists of autochthonous *Palaeonucula makitoensis* and *Solemya suprajurensis* in association with reworked individuals of free-living *Entolium inequivalve* and byssate *Limatula iwayae*. These genera are typical of Jurassic mid-to outer-shelf and oxygen-controlled environments (Aberhan, 1994). Moreover, Recent representatives of *Solemya* live in muddy bays of stagnant water conditions and in deep-sea areas characterized by low oxygen levels, and are components of the chemosynthetic community (Reid and Bernard, 1980; Felbeck *et al.*, 1981). Therefore, the low diversity of this assemblage probably is a result of lowered oxygen levels within the sediment.

Furthermore, this assemblage is associated with the grazing traces (pascichnia) *Spirophycus* and *Phycosiphon*, whereas dwelling traces (domichnia) such as *Skolithos* and *Palaeophycus* are absent. These pascichnia exhibit a low-diversity, moderately high density and small size, suggestive of opportunistic producers (Bromley, 1996). Ekdale and Mason (1988) proposed that pascichnia-dominated trace fossil assemblages are formed under less oxygenated conditions than domichnia-dominated ones. Hence, the character of the ichnofauna supports our interpretation of relatively low oxygen-conditions.

## Conclusions

1. Three bivalve assemblages are distinguished in the Jurassic Mitarai Formation, Tetori Group. The *Modiolus maedae*-*Tetorimyia carinata* assemblage contains abundant semi-infaunal and deep-burrowing taxa in preserved life orientation and represents the undisturbed, autochthonous fauna of inner shelf environments. The *Entolium inequivalve* assemblage occurs in outer shelf deposits and is characterized by a mixture of autochthonous infaunal ele-

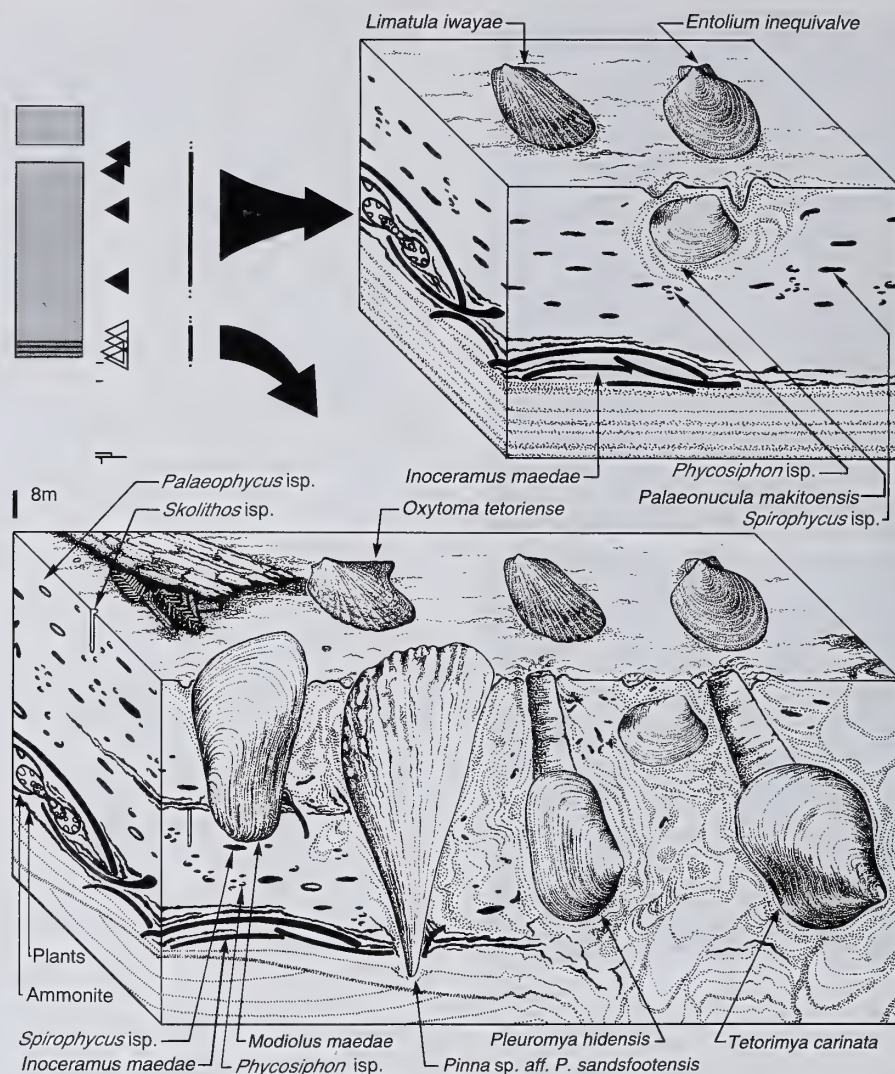


Figure 7. Ecological reconstruction of the bivalve fauna in shelf deposits of the Mitarai Formation.

ments and parautochthonous byssate or free-living epifauna. The *Inoceramus maedae* assemblage consists of fragments and disarticulated valves and represents typical allochthonous occurrences. In particular *Inoceramus maedae* underwent transport from sandy nearshore areas.

2. The *Entolium inequivalve* assemblage contains the chemosymbiotic bivalve *Solemya*, and is associated with a low-diversity ichnofauna, which suggests lowered oxygen conditions.

3. Palaeoecological and taphonomic data allow a more refined reconstruction of palaeoenvironments and their changes through time than sedimentary features alone.

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## Regular axopodial activity of *Diplosphaera hexagonalis* Haeckel (spheroidal spumellarian, Radiolaria)

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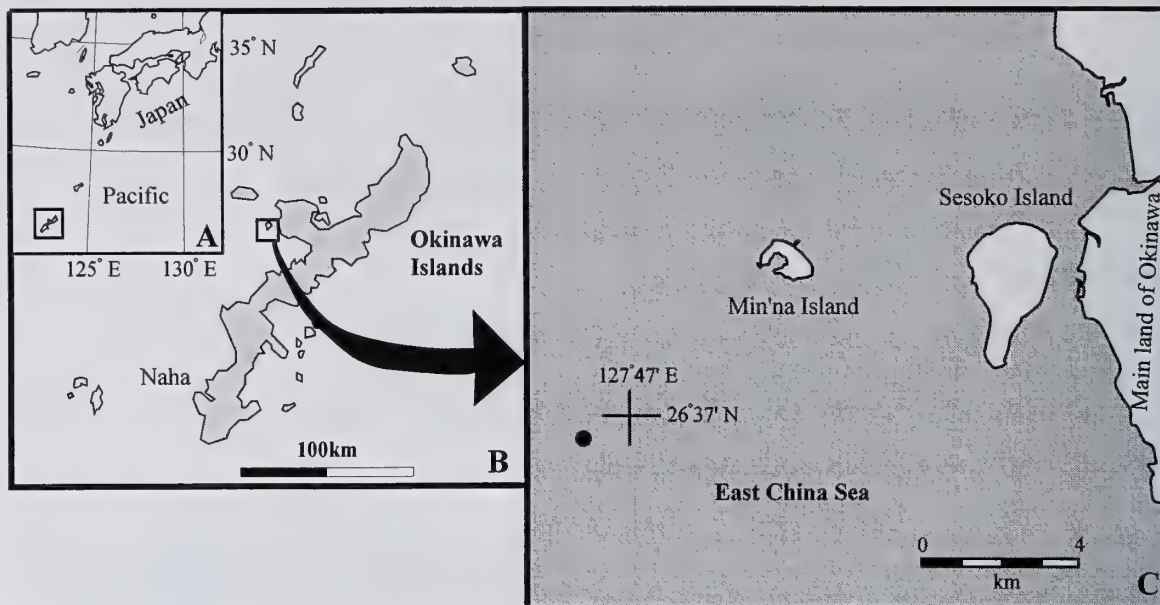
**Abstract.** The physiological ecology of a spherical polycystine species, *Diplosphaera hexagonalis* collected from the surface water of the Kuroshio Current in the East China Sea off Sesoko Island, Okinawa, was observed in a culture dish for three days. The observed specimen demonstrated cyclic extension and contraction of axopodia by a regular interval of ca. 630 seconds. Each cycle was divided into four phases based on the state of the axopodia and movement of axopodial vacuoles. Vertical migration in response to axopodial motility was also observed. The specimen began to rise accompanied with the axopodial extension, floated in the seawater and often moved horizontally when its axopodia were radiated symmetrically, and began to sink in correspondence with the axopodial contraction. The effect of thermal currents on this behavior is easily neglected on the ground of the definite coincidence with the rhythmic extension and contraction of axopodia. The rhythm appears to play important roles in the physiological ecology of this species, including food capture and possibly buoyancy. The taxonomic section presents a nearly complete synonym list of *D. hexagonalis* and summarizes that the genus *Diplosphaera* is a senior synonym of *Astrosphaera*, *Drymosphaera* and *Leptosphaera*. Thus, *Diplosphaera hexagonalis* is the only valid name for this species, according to ICZN Article 55.3. *Diplosphaera* is considered herein to belong not to the family Actinommiidae but to the Astrosphaeridae, unlike in most previous paleontological and biological studies. The family Macrosphaeridae Hollande and Enjume, 1960, to which the genus *Diplosphaera* was assigned, is treated as an invalid name because the type genus *Macrosphaera* has not been established yet.

**Key words:** axopodia, *Diplosphaera hexagonalis*, East China Sea, living radiolaria, Okinawa, physiological ecology

### Introduction

Radiolaria is an informal taxonomic group of planktonic unicellular Protocista generally possessing a plane, line or point skeletal symmetry of the test. This group includes the classes Polycystina possessing a siliceous test, Acantharia with a strontium sulfate test, and Phaeodaria having a siliceous test with incorporated organic substances (Margulis and Schwartz, 1988; The Committee on Systematics and Evolution of the Society of Protozoologists, 1980). Of these radiolarians, solitary spheroidal Polycystina ranges in age from the middle Cambrian to the present (Nazarov, 1988). Since the polycystine group is widely distributed in the open oceans, information on its physiological ecology will provide new insights both in analysis of paleoceanographic analyses and the establishment of a natural classification.

Although previous studies have revealed detailed information on physiological and ecological information (living features, longevity, prey, and skeletal growth under culture conditions and some fine structures) of some discoidal spumellarians such as *Dictyocoryne truncatum* (Ehrenberg) and *Spongaster tetras* (Haeckel) (e.g. Anderson *et al.*, 1989a, 1989b; Anderson and Matsuoka, 1992; Matsuoka, 1992; Matsuoka and Anderson, 1992; Sugiyama and Anderson, 1997), we know little about the physiological ecology of spheroidal spumellarians. Examination of the cytological structures of solitary spherical polycystines has provided some groundwork for these analyses (Anderson, 1976, 1981, 1983; Anderson *et al.*, 1998; Cachon and Cachon, 1972a, 1972b, 1976, 1985; Haeckel, 1862; Haecker, 1907; Hertwig, 1879, 1932; Hollande and Enjume, 1954, 1960; Hollande *et al.*, 1965; Swanberg *et al.*, 1990),



**Figure 1.** Sampling location. **A.** A map showing the position of Okinawa Islands (open square). **B.** The Okinawa Islands and its adjacent islands. **C.** The sampling location (solid circle).

but there have been only limited investigations of the nutritional role of symbionts (Anderson *et al.*, 1983, 1985) and the possible reproductive role of swarm cells released by mature specimens during laboratory culture (Anderson, 1978, 1984 and others).

In order to observe living features of radiolarians in the surface seawater of the Kuroshio Current, some Japanese radiolarian paleontologists have collaborated on observation tours of living organisms at the Sesoko Tropical Biosphere Research Center (STBRC), University of the Ryukyus, Sesoko Island, Okinawa Prefecture, Southwest Japan, since 1997 (Figure 1). During the 2nd tour held on October 5th to 14th, 1998, we made three samplings on October 7th, 8th and 12th, 1998, and encountered approximately 40 species in laboratory examinations. As a result, we obtained extensive information about their pseudopodial behavior using normal still and video photography.

Among the observed radiolarians, we particularly traced continuous axopodial activity of one specimen of *Diplosphaera hexagonalis* Haeckel, a solitary spheroidal spumellarian representative of the observed radiolarian fauna, during four days from October 7th to 10th, 1998. Our interest was especially aroused since it systematically repeated axopodial extension and contraction cycles at regular intervals. In this report, we present a detailed description of the features of the extension and contraction cycles and possible implication for the physiological ecology of *D. hexagonalis* in relation to this cyclical axopodial activity. A probable physiological function and an explanation of a mechanism of the cycles are also discussed. This paper also describes the taxonomic classification of *D. hexagonalis* in order to resolve the confusion surrounding its generic and family positions.

## Materials and methods

Plankton samples containing the observed *Diplosphaera hexagonalis* were collected on October 7th, 1998, at a locality (Station 1; Figure 1) approximately 12 km west of Sesoko Island and more or less affected by the warm-water Kuroshio Current. Ambient seawater temperature and salinity at the sampling location were 28.5 °C and 34.0 ‰, respectively. The sample was collected by 3 min. tow using a 36 µm mesh net. On return to the laboratory at STBRC, small portions of the sample were placed into sorting dishes, examined with binocular microscopes, and each individual radiolarian was separated from other matter using a Pasteur pipette into a glass vial (ca. 25 mm diam. ×50 mm tall), a glass culture dish (50 mm or 90 mm diam.) or a single well of a multiwell tissue culture plate (23 mm diam. ×20 mm tall) (FALCON® 3043, Becton Dickinson Labware, Lincoln Park, N. J.) previously filled with ambient seawater from the sampling location. These culture containers with radiolarians were placed either in a temperature-controlled bath with fluorescent light units or in temperature-uncontrolled baths without fluorescent light units. The temperature of the former bath was kept at 28 °C by a heater-chiller balance, whereas that of the latter was about 27 °C, the room temperature of the laboratory, throughout the culture work. Both types of baths were covered by metal foil during the night to produce a day/night cycle. The radiolarians were cultured without exchange of the seawater, no supply of food, nor removal of any filth.

Continuous axopodial activity of one *D. hexagonalis* individual was observed from October 7th to 10th October, 1998, using Nikon Diaphot and Olympus CK2 inverted microscopes, mainly following previously established protocols

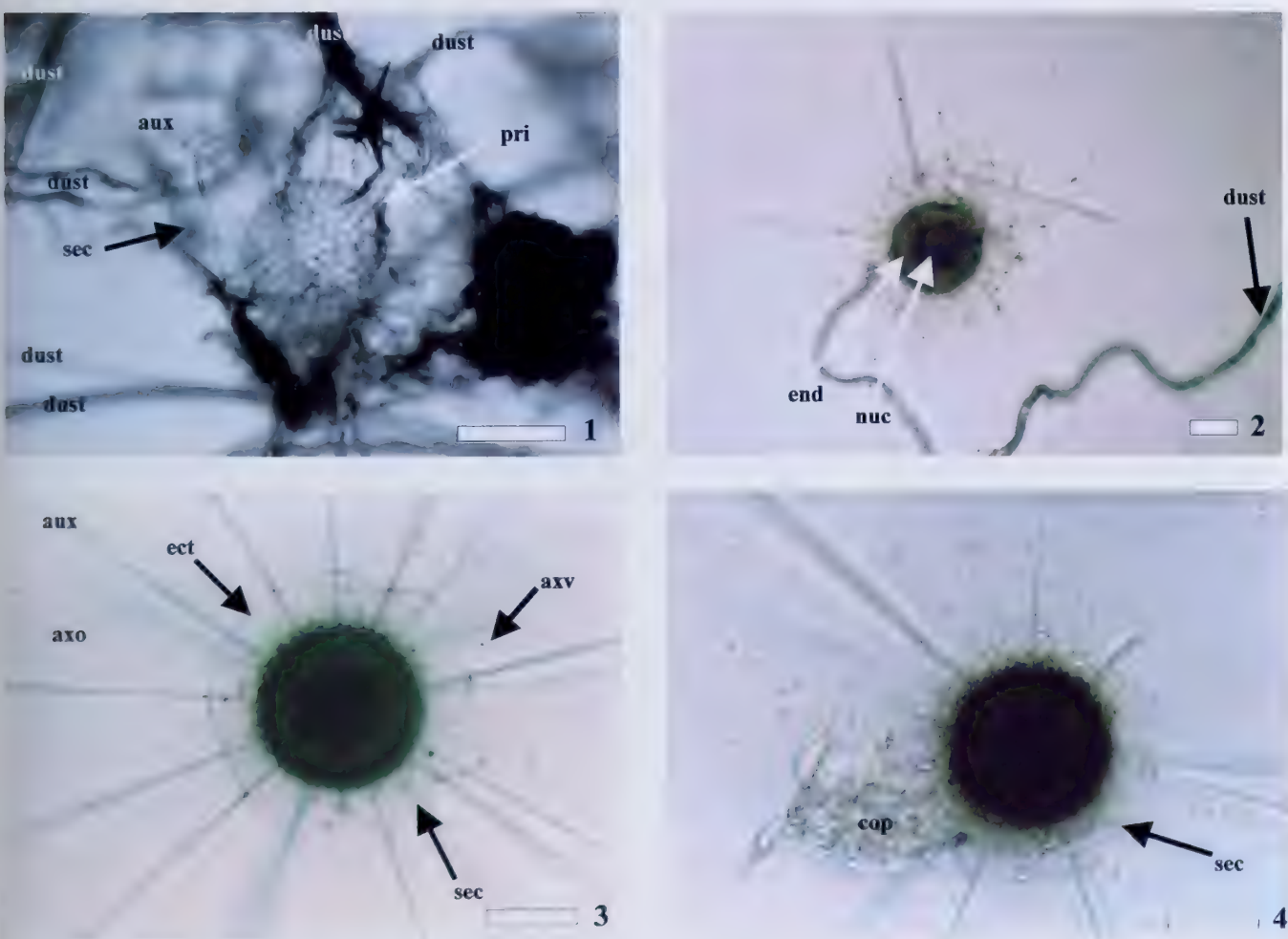


(Anderson *et al.*, 1989a). We used a video camera (SONY HANDYCAM DCR-TRV9), with a resolution of 0.76 million pixels, attached to the Nikon Diaphot microscope through a TV adapter and digital camera (FUJIFIX HC-300) in order to record vivid images of radiolarian activity. The observations were recorded on five 60-minute videotapes and more than 10 pictures. Only for one individual was the continuous axopodial activity described in this paper ascertained. Although six to ten other individuals were observed with two inverted microscopes for snapshots using normal cameras as well, we did not confirm whether other specimens show continuous axopodial behavior or not.

### Observational results of living *Diplosphaera hexagonalis*

The skeleton of *Diplosphaera hexagonalis* (Figure 2.1) consists of one spherical primus exosphere, one polyhedral secundus exosphere with triangular frameworks, and a dozen triradiate auxiliary spines radiating from the primus exosphere (for skeletal terms see Suzuki, 1998). This species was assigned to the family Astrosphaeridae based on criteria published by Hollande and Enjume (1960).

Living *D. hexagonalis* possesses a dark, grayish red, spherical cell body within the secundus exosphere, and fine, transparent axopodia radiating from the surface of the cell body (Figure 2.2, 2.3). The spherical cell is composed of



**Figure 2.** General view of *Diplosphaera hexagonalis* Haeckel. 1. Light transmitted microscopic photograph. 2-4. Inverted microscopic photographs, showing a bottom view. Scale bars are equal to 100  $\mu$ m. 1. Skeleton structure of *D. hexagonalis* possessing a spherical primus exosphere (pri) and a polygonal frame of the secundus exosphere (sec). These two shells are connected with numerous auxiliary spines (aux). 2. Numerous yellow-brown axopodial vacuoles surround the endoplasm. Axopodia may begin to extend (EII subphase). 3. This specimen has a small amount of axopodial vacuoles. Both the fine axopodia and axopodial vacuoles near the endoplasm indicate that this specimen is in the EI subphase. 4. A copepod attached to *D. hexagonalis* is partially digested by the specimen. Abbreviations: nuc, nucleus; end, endoplasm; cop, copepod; ect, ectoplasm; axo, axopodia; aux, auxiliary spine; axv, axopodium vacuole; pri, primus exosphere.

two parts: (1) a more transparent light-colored, bubble-like outer part between the primus and secundus exospheres, corresponding to ectoplasm, and (2) a more opaque, spherical inner part within the primus exosphere. The latter is further subdivided into a deeper-colored central part, and the surrounding endoplasm which is slightly lighter-colored. The inner part is referred to as a nucleus according to Hollande and Enjume (1960).

The length of the axopodia changes periodically from a minimum of 0.12–0.13 mm to longer than 2.0 mm. Vacuoles, dark amber or reddish gray in color, globular in shape and of a few to ten  $\mu\text{m}$  in diameter are displayed on each axopodium. The total number of vacuoles varies among specimens but it typically is about 200. The distribution of the vacuoles on the axopodia changes with the length of the axopodia. The biological function and physical composition remains unknown.

We observed the specimen with a copepod (ca. 400  $\mu\text{m}$  in length) attached to its axopodia outside the secundus exosphere at noon on the 7th (Figure 2.4). On the next day, the entrails of the copepod began to dissolve, and the entire copepod body completely disappeared on October 9th. After the digestion of the copepod, the ectoplasm of *D. hexagonalis* increased in volume to fill the secundus exosphere. During the observations, other organisms, probably ciliates, moved around the halo of axopodia of *D. hexagonalis*, and became momentarily immobilized on the axopodia. However, all of these microorganisms were soon released by the shortening of the axopodia. This seems to indicate that these microorganisms were not captured but only snared accidentally. Some of the microorganisms escaped from *D. hexagonalis*, but those which failed to escape from the specimen were again snared by the axopodia.

#### Systematic repetition pattern of axopodial extension and contraction

On October 9th, a series of 17 extension and contraction cycles of the axopodia was observed over a duration of 2 hrs. 44 min. 21 sec. (Figure 4). The cycles described herein have a reasonably regular interval; the longest interval was 677 sec, the shortest 550 sec and the mean 633 sec. Each cycle is divisible into four phases based on the state of the axopodia and movement of axopodial vacuoles. These phases are as follows: S-phase (short phase, Figures 3.1, 5), E-phase (extension phase, Figures 3.2–3.5, 5), L-phase (long phase, Figures 3.6–3.7, 5) and C-phase (contraction phase, Figures 3.8–3.12, 5). Among them, the E-phase is further subdivided into three subphases (EI-subphase, EII-subphase and EIII-subphase), and the C-phase into two subphases (CI-subphase and CII-subphase). Although each cycle has almost the same interval, as mentioned above, phase and subphase intervals in each cycle differ considerably as shown in Figure 4. We tried to interrupt the axopodial movement by vibrations produced by tapping the dish with sticks but the cyclicity was uninterrupted, and what is more, the regularity was maintained in spite of contact by ciliates and other small organisms.

**S-phase** (Figure 3.1).—This phase is defined as an interval after C-phase, during which axopodial length is at a mini-

mum. Axopodia in this phase are composed of two kinds; one is named H-index type and the other is L-index type. The former type of axopodia has relatively high refractive index against seawater under the microscope, whereas the refractive index of the latter type is lower. Usually, H-index type axopodia are shorter than the L-index type in this phase. The length of the H-index type axopodia is about half of the primus exosphere diameter, while that of the L-index type axopodia is approximately double that of the H-index type. In this phase, most vacuoles on both types of axopodia are rarely moved outside the ectoplasm. The shortest interval of this phase is 4 sec, the longest 18 sec and the mean 12 sec.

**E-phase.**—This phase is defined as an interval after S-phase, during which most axopodia are extending. The shortest interval of this phase is 160 sec, the longest 474 sec and the mean 302 sec. The E-phase is subdivided into the following EI-, EII- and EIII-subphases.

During the EI-subphase, we still cannot see the outward movement of the axopodial vacuoles situated in the secundus exosphere (Figure 3.2). In contrast, vacuoles on the L-index type axopodia begin to move slowly inwards. H-index type axopodia begin to extend slowly and become more slender. The refractive index of both types of axopodia decreases with their extension. During this subphase, the difference between the L- and H- type axopodia becomes indistinct. The shortest interval of this subphase is 14 sec, the longest 86 sec and the mean 31 sec.

The EII-subphase starts by the outward movement of axopodial vacuoles, and ends by the event that the distal parts of axopodia become invisible (Figure 3.3). Within this subphase the axopodia maintain a continuous and slow extension. Most axopodial vacuoles continue to move outward, but a few return to the inside of the secundus exosphere. The shortest interval of this subphase is 2 sec, the longest 140 sec and the mean 85 sec.

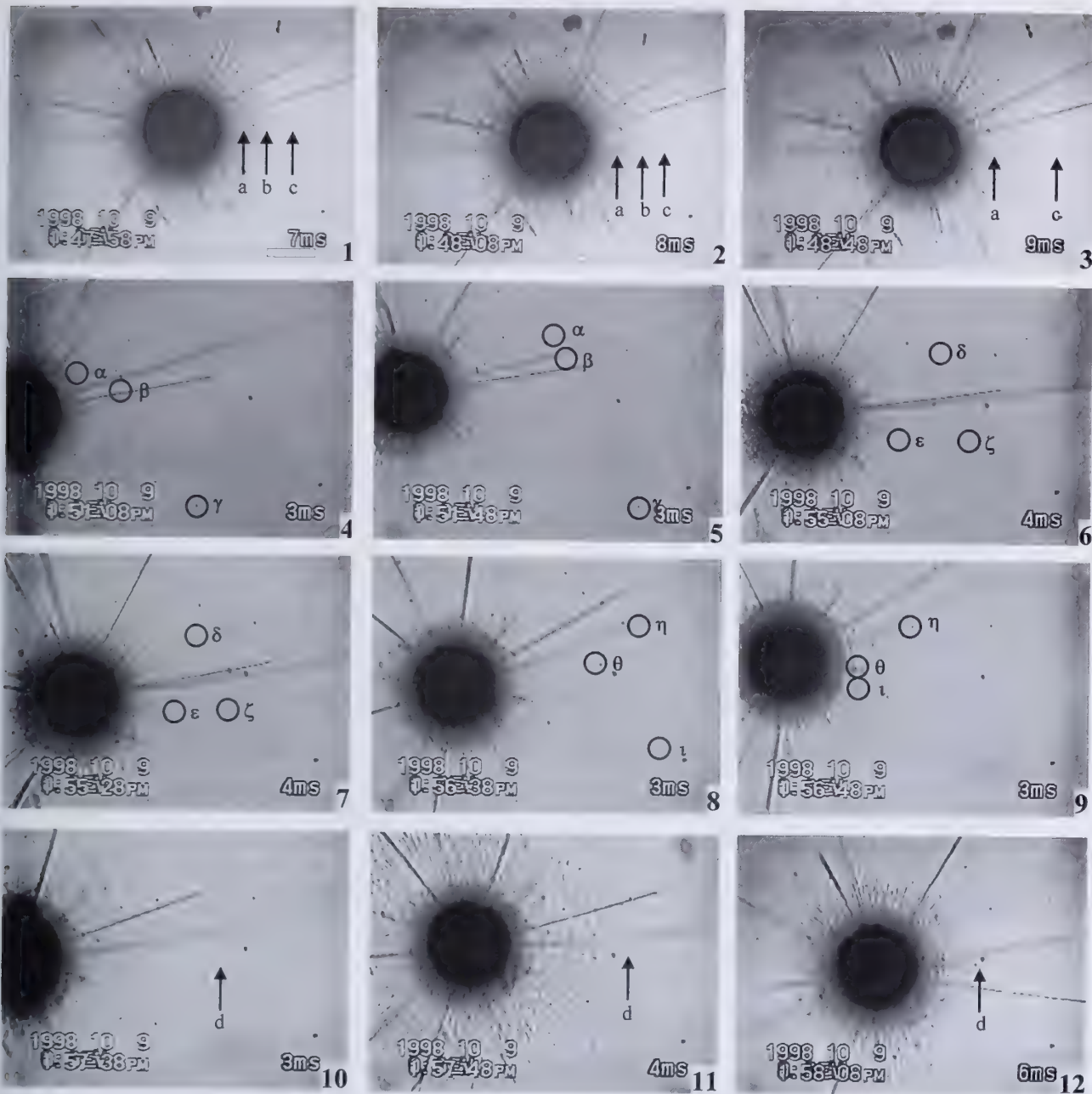
The end of the subsequent EIII-subphase is defined by unrecognizableness of the outward extension of axopodia (Figure 3.4, 3.5). During this subphase, the distal parts of axopodia are invisible but the outward extension can be discerned by the movement of axopodial vacuoles. The shortest interval of this subphase is 46 sec, the longest 433 sec and the mean 217 sec.

**L-phase** (Figure 3.6, 3.7).—This phase is defined as an interval during which the specimen keeps radiate, long axopodia with immobile vacuoles. Axopodia in this phase are finer than those in the S-phase, and the refractive difference between the axopodia and seawater is negligible. Axopodial vacuoles are heterogeneously distributed around the halo of axopodia. The shortest interval of this phase is 29 sec, the longest 205 sec and the mean 100 sec.

**C-phase.**—This phase subsequent to the L-phase is marked by an abrupt contraction of axopodia towards the endoplasm, and ends when most axopodia finish shrinking. The shortest interval of this phase is 59 sec, the longest 282 sec and the mean 168 sec. This phase is subdivided into CI- and CII-subphases as follows.

In the CI-subphase, axopodial vacuoles begin to be moved back to the ectoplasm although the axopodia are not





**Figure 3.** Four phases of extension and contraction of the axopodia. Scale bar is equal to 100  $\mu\text{m}$ . 1. S-phase. 2. E1-subphase. 3. E2-subphase. 4, 5. E3-subphase. 6, 7. L-phase. 8, 9. C1-subphase. 10–12. C2-subphase. Arrows: a, the periphery of the dominant axopodial vacuoles; b, the distal part of H-index type axopodia; c, the distal part of L-index type axopodia; and d, the distal part of the contractile axopodia. Open circles with Greek symbols in Figure 3.4–3.9 represent axopodial vacuoles. The same Greek symbols in different figures imply the same axopodial vacuole.

yet contracted (Figure 3.8, 3.9). During this subphase the refractive index of the axopodia increases gradually accompanied by thickening of the axopodial diameter at the proximal point where it attaches to the cell body. A few axopodial vacuoles are moved inward relatively quickly. These vacuoles pass the secundus exosphere and reach

near the surface of endoplasm. The shortest interval of this subphase is 34 sec, the longest 227 sec and the mean 133 sec.

The C2-subphase is characterized by an abrupt contraction of axopodia and followed by the S-phase after complete cessation of axopodial shrinking. At the beginning of this

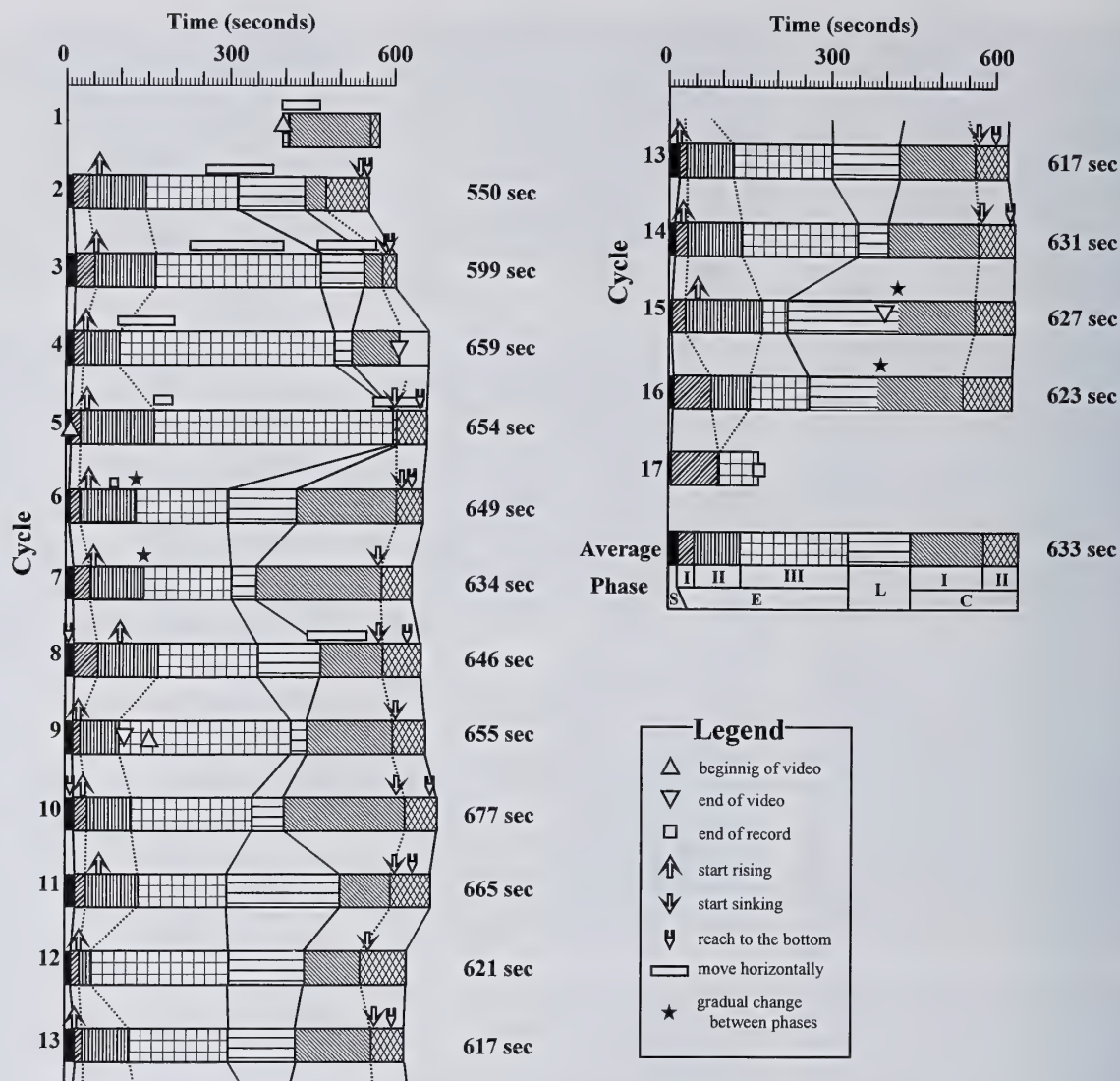


Figure 4. Diagram illustrating the four phases of the axopodia on 9th, Oct, 1998.

subphase, the periphery of the axopodia shrinks suddenly (arrow d in the Figure 3.10–3.12). The vacuoles on the distal part of the axopodia are moved inwards by this action, and the refractive index of the axopodia increases immediately (Figure 3.10). Subsequently, the axopodia shorten in a stepwise fashion with a concomitant increase of the refractive index at each step. The axopodial vacuoles are also moved inwards in the same stepwise fashion. The halo of axopodia in this subphase has a gelatinous spherical envelope with numerous pigmented dots (Figure 3.11). The shortest portion of this subphase is 25 sec, the longest 90 sec and the mean 64 sec.

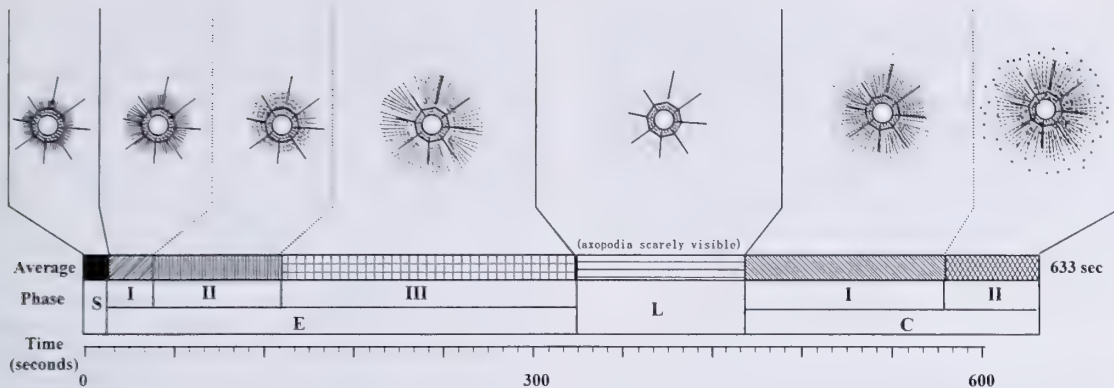
#### Vertical migration in connection to axopodial motility

During the observation of *Diplosphaera hexagonalis*, we found that rising, floating and sinking motions in the culture vessel are always related to axopodial extension and contraction. Vertical migration was confirmed with video re-

cords and was counted 14 times at each expansion and contraction rhythm of the axopodia except for the last two rhythmic cycles which were not recorded on the video tape (Figure 4). It would be doubtful if this behavior depended on the effect of thermal currents in the observed dish, but the possibility of this effect is easily discarded: the relation of floating and sinking correlated with the changes in axopodial rhythm is so strict, and the radiolarian specimen did not show any other irregular rising and sinking movement in spite of particular careful observation as shown in Figure 4.

The specimen begins to rise from the bottom of the vessel during the interval from the middle EI-subphase to early EII-subphase accompanied with the axopodial extension (the up-arrows in Figure 4). Cessation of this movement is quite gradual. The specimen floats in the seawater and often moves horizontally during the EII-subphase through the middle CII subphase (the open rectangles in Figure 4). When the specimen is floating, its axopodia are radiated symmetri-





**Figure 5.** Schematic illustration of the cycle of extension and contraction of the axopodia. Solid thick line: siliceous skeleton. Solid fine line: H-index type axopodia. Dark gray small dot: axopodium vacuole. Dark to light gray fine lines: L-index type axopodia. The darkness of lines indicates a refractive index between the axopodia and the seawater.

cally from the cell body, which drifts in all directions very slowly. Around the late CI-subphase to the early CII-subphase, the specimen begins to sink in correspondence with the axopodial contraction (the down-arrows in Figure 4). After a few to 60 seconds, the body of the specimen reaches the bottom of the culture vessel.

### Discussion

Although a rhythmic extension and contraction of radiolarian axopodia has been reported by Anderson (1983), the observation herein is the first evidence showing a regular rhythm of axopodial movement at approximately ten and a half-minute intervals. Our observation demonstrated that videotape recording is a fairly useful and advanced method by which to document the continuous activities of radiolarian axopodia. We accumulated a continuous record of *D. hexagonalis* with cyclic axopodial motions only from one specimen using videotapes, but other collected specimens (more than ten specimens) also appeared to have the same kind of rhythmical activity, judging from a series of still photograph images. Consequently, we can conclude that the above described cyclical motions are a common physical behavior of *D. hexagonalis*.

Spherical symmetry is probably not a major predictive factor in the occurrence of the regular, cyclical axopodial contractions observed in *D. hexagonalis*. Several spherical spumellarian species of genera with a double shell (e.g. *Hexacanthium* spp. and *Spongodymus* sp. indet.) also were observed during this experiment, but they never exhibited a similar rhythmic motion of the axopodial array. Likewise, other protista, including Acantharia and Heliozoa, have a symmetric distribution of axopodia around the cell body, but we have no information if they possess possible cyclical patterns as observed in *D. hexagonalis*. Currently, therefore, we can infer that the observed regular rhythm is peculiar to *D. hexagonalis* and its related taxa, and that a particular cytological apparatus of *D. hexagonalis* likely produces this rhythm.

The cytology of *D. hexagonalis* is unusual. There is no axoplast and the nucleus is surrounded by large vacuoles

(Hollande and Enjume, 1960). However, as with other axopodial-bearing species, the axopodium contains an array of axially oriented internal microtubules (axoneme). An axoplast is absent also in other spherical polycystine genera including *Rhizoplegma*, *Centrocubus*, *Octodendron* and *Haplospira* (Cachon and Cachon, 1985). It is not known presently whether the absence of an axoplast is related to the regular rhythmic cycles of extension and contraction of the axopodia in *D. hexagonalis*. When the axoplast is present in other species, it is rich in tubulin monomers that polymerize to form microtubules and is usually located centrally where the microtubules of the axonemes converge. Hence, the axoplast may provide an organizing center for the axonemes. In the absence of an axoplast, the regular array of large vacuoles in *D. hexagonalis* could serve to support the axonemes and in addition may contribute to the cytoplasmic volume as the periphery array of axopodia expands. If the expansion of the axopodial array indeed contributes to enhanced buoyancy, then there must be a source of additional cytoplasmic volume to supply the added low-density mass produced by the expansion of the peripheral corona of axopodia. If the expanding axopodia were simply constructed at the expense of existing cytoplasmic mass in the main cell body, without further expansion of internal volume, there would be no net gain in buoyancy. If, however, the vacuoles increase in size as the axopodia expand, this could result in less mass per unit volume, and produce an increased buoyancy. Likewise, according to this model, as the axopodia contract, the vacuoles may decrease in volume, thus accommodating the inward flow of cytoplasm toward the central body and producing a concomitant decrease in buoyancy. A dynamic adjustment in volume by the central vacuoles may provide a necessary mechanism for maintaining appropriate mass balance required to control buoyancy as the peripheral axopodial array expands and contracts. The rhythmic extension and contraction of the axopodia appear to play important roles in the physiological ecology and physical functioning of *D. hexagonalis*, including food capture and possibly the regulation of buoyancy as reported here.

The extension of protozoan axopodia usually occurs by



elongation of the microtubules when additional tubulin is polymerized at one end and they are shortened by disassembly of the tubulin, all in response to biochemically regulated cycles (e.g., Tilney and Byers, 1969). To understand the mechanism of the observed rhythmic extension and contraction of axopodia, it is essential to investigate more thoroughly changes in cytological structures and correlated biochemical processes with the aim of creating a more complete model of the rhythmic activity of axopodia in *D. hexagonalis*.

### Systematic description

Family Astrosphaeridae Haeckel 1882,  
sensu Hollande and Enjumet 1960  
Genus *Diplosphaera* Haeckel 1860, emend.  
Hollande and Enjumet, 1960

*Type species.*—*Astrosphaera gracilis* Haeckel 1862, designated by Campbell (1954).

*Diplosphaera* Haeckel, 1860, p. 804; Haeckel 1887, p. 246; Campbell, 1954, D.62; Hollande and Enjumet, 1960, p. 116; Kozur and Mostler, 1979, p. 12.

*Astrosphaera* Haeckel 1887, p. 250; Campbell, 1954, D61.

*Drymosphaera* Haeckel 1882, p. 452; Haeckel 1887, p. 248; Campbell, 1954, D.62.

*Leptosphaera* Haeckel, 1887, p. 243-244; Campbell, 1954, D.62.

*Remarks.*—*Diplosphaera* is regarded as the senior synonym of three other genera, *Astrosphaera*, *Drymosphaera* and *Leptosphaera*, based on the ontogenetic growth change of their skeletal structures and similarity of their cytological structures (Hollande and Enjumet, 1960). According to them, the *Leptosphaera*-form, the youngest, possesses two exospheres without by-spines. *Diplosphaera*- and *Drymosphaera*-forms appear in the next ontogenetic growth stage through the development of by-spines on one of these. When both exospheres have by-spines, this form is referred as an *Astrosphaera*-form.

*Diplosphaera* has been assigned to three different families: classical studies described it as a member of the Astrosphaeridae Haeckel 1882 (e.g. Haeckel, 1882, 1887; Campbell, 1954; Mast, 1910). Recent paleontologists and paleoceanographers prefer to assign it to the Actinommidae Haeckel 1862 (e.g. Kozur and Mostler, 1979; Takahashi, 1991). Finally, cytological researchers have regarded it as a member of "Macrosphaeridae" Hollande and Enjumet 1960 (e.g. Anderson, 1983; Cachon and Cachon, 1985; Hollande and Enjumet, 1960). However, since *Macrosphaera* had not been proposed as a genus name, the family name "Macrosphaeridae" violates Art 29.1 of ICZN (1999), which states that a family-group name is formed by adding the termination -idae to the stem of the name of the type genus, or to the entire name of the type genus. *Diplosphaera* is cytologically closely similar to the genus *Haplosphaera* Hollande and Enjumet 1960, the type genus of the "Macrosphaeridae" (Hollande and Enjumet, 1960). The phylogenetically close relationship between *Diplosphaera* and *Haplosphaera* suggests that the family

"Macrosphaeridae" is included in the Astrosphaeridae.

Hollande and Enjumet (1960) revealed that the genus *Actinomma* Haeckel 1862, the type genus of the Actinommidae, is one of the centroaxoplastid spumellarians with the axoplast enclosed by the nuclear membranous envelope, whereas the genus *Diplosphaera* of the Astrosphaeridae belongs to the anaxoplastid spumellarians without axoplast. This cytological difference between the Actinommidae and Astrosphaeridae suggests that *Diplosphaera* does not belong to the Actinommidae.

Almost all species assigned to *Diplosphaera* have been recovered from surface sediment or plankton samples due to their fragile skeletons. Only one species, *Drymosphaera* ? *pseudosagenoscena* Sugiyama 1992, is known from the lower Miocene (Sugiyama, 1992). All assigned species other than *D.?* *pseudosagenoscena* lack a microsphere, so that the lower Miocene species appears to belong to another genus.

*Range.*—Recent as far as known.

*Known occurrence.*—Equatorial and North Pacific, equatorial Atlantic and Mediterranean.

### *Diplosphaera hexagonalis* Haeckel, 1887

*Diplosphaera hexagonalis* Haeckel 1887, p. 246, pl. 19, fig. 3; Hollande and Enjumet, 1960, p. 116, pl. 12, fig. 6, pl. 15, fig. 11, pl. 23, fig. 2, pl. 26, fig. 2; Cachon and Cachon, 1972a, pl. 35, figs. b, c; Anderson, 1983, p. 66-67; Fujioka, 1990, p. 136, pl. 39, fig. 7.

*Astrosphaera hexagonalis* Haeckel 1887, p. 250, pl. 19, fig. 4; Mast, 1910, p. 52; Popofsky, 1912, p. 105-106, text-fig. 16, pl. 8, fig. 2; Sugano, 1937, p. 64, figs. 21; Renz, 1976, p. 100-101, pl. 2, fig. 12; Tan and Tchang, 1976, p. 229, figs. 4a, b; Takahashi and Honjo, 1981, p. 147, pl. 2, fig. 12; Nishimura and Yamauchi, 1984, p. 24, pl. 14, figs. 1, 2; Boltovskoy and Jankilevich, 1985, pl. 1, fig. 17; Yamauchi, 1986, pl. 2, fig. 3; Fujioka, 1990, p. 136, pl. 38, fig. 7; Yeh and Cheng, 1990, pl. 3, fig. 2; Takahashi, 1991, p. 69, pl. 11, figs. 1-3; Boltovskoy, Alder and Abelman, 1993, p. 1891; Tan, 1998, p. 164, figs. 152a, b (= the same figures of Tan and Tchang, 1976); Boltovskoy, 1998, p. 41, figs. 15-40.

*Leptosphaera hexagonalis* Haeckel 1887, p. 244, pl. 19, fig. 2. [nomen oblitum]

*Remarks.*—Most previous authors have identified *D. hexagonalis* as a species of *Astrosphaera*. As mentioned in the generic remarks, *Astrosphaera* is a junior synonym of the genus *Diplosphaera* (Hollande and Enjumet, 1960; Kozur and Mostler, 1979), which means that *Astrosphaera hexagonalis* is an unavailable name (Article 53.3 of ICZN, 1999). Thus, *Diplosphaera hexagonalis* is the valid name of this species.

Skeletal residues are obtained from surface sediment in the eastern Pacific Ocean, China Sea, and the Mediterranean (Tan and Tchang, 1976; Nishimura and Yamauchi, 1984), whereas they are not found in the sediment from the center of the equatorial Pacific (Renz, 1976; Takahashi, 1991). The skeleton of this species appears to dissolve easily at greater water depth as discussed by Takahashi (1991).



*Known Range*.—Recent.

*Occurrences*.—Equatorial Pacific, equatorial Atlantic, East China Sea, South China Sea, east off Okinawa, Shikoku and Taiwan, Mediterranean and west Patagonia.

*Habitat*.—Warm seawater. Surface to 300 m depth (Hollande and Enjumet, 1960; Renz, 1976).

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- ◎第151回例会は、2002年1月26日（土）、1月27日（日）に鹿児島大学理学部で開催されます。1月27日（日）午後に公開講演として「21世紀は自然史の時代 ―古生物学・フィールド科学からの提言―：世話人、森 啓・矢島道子」を実施致します。一般講演の申し込み締切は11月30日（金）です。
- ◎2002年年会・総会（2002年7月上旬開催予定）には福井県立恐竜博物館から開催申し込みがありました。また、第152回例会（2003年1月下旬開催予定）には横浜国立大学教育人間科学部から開催申し込みがありました。
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## CONTENTS

<b>Mohamed Zakhera, Ahmed Kassab and Kiyotaka Chinzei:</b> <i>Hytissocameleo</i> , a new Cretaceous oyster subgenus and its shell microstructure, from Wadi Tarfa, Eastern Desert of Egypt .....	77
<b>Michiko Saito and Kazuyoshi Endo:</b> Molecular phylogeny and morphological evolution of laqueoid brachiopods .....	87
<b>Fumihisa Kawabe and Yasunari Shigeta:</b> The genus <i>Hourcquia</i> (Ammonoidea, Pseudotissotiidae) from the Upper Cretaceous of Hokkaido, Japan: biostratigraphic and biogeographic implications .....	101
<b>Masayuki Ehiro:</b> Some additional Wuchiapingian (Late Permian) ammonoids from the Southern Kitakami Massif, Northeast Japan .....	111
<b>Shuji Niko:</b> Middle Carboniferous orthoconic cephalopods from the Omi Limestone Group, Central Japan .....	115
<b>Toshifumi Komatsu, Ryo Saito and Franz T. Fürsich:</b> Mode of occurrence and composition of bi-valves of the Middle Jurassic Mitarai Formation, Tetori Group, Japan .....	121
<b>Noritoshi Suzuki and Kazuhiro Sugiyama:</b> Regular axopodial activity of <i>Diplosphaera hexagonalis</i> Haeckel (spheroidal spumellarian, Radiolaria) .....	131
<b>PROCEEDINGS</b> .....	141

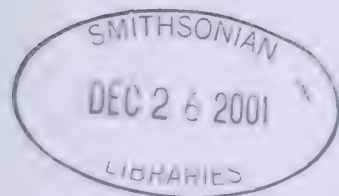


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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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## Ostracode biostratigraphy of the Lower Cretaceous Wakino Subgroup in northern Kyushu, Japan

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**Abstract.** Nonmarine ostracodes from the Lower Cretaceous Wakino Subgroup in northern Kyushu were studied biostratigraphically. Analysis of abundant fossil ostracodes has led to recognition of 11 assemblages and subassemblages. Vertical changes of these assemblages have made possible biostratigraphical zonation by ostracodes as follows: the *Darwinula* a. z. (assemblage zone), the transitional a. z. and the large Cypridacean a. z. in ascending order. Using this zonation, the formations of the Wakino Subgroup in the eastern area are correlated with those in the western type area.

**Key words:** Biostratigraphy, Lower Cretaceous, Northern Kyushu, ostracodes, southwest Japan, Wakino Subgroup

### Introduction

The correlation of Lower Cretaceous nonmarine sediments is controversial in Eastern Asia, because their relations with marine sediments are known only in restricted regions (Matsukawa and Obata, 1992, 1994). The same is true in Japan. Molluscan fossils have been traditionally used in the correlation of Cretaceous strata of Japan by many investigators (Kobayashi and Suzuki, 1936; Ota, 1960; Hase, 1960; etc.). This approach is not reliable due to the fact that the same molluscan assemblages and characteristic species occur in several different horizons showing similar depositional environments (Matsukawa and Ito, 1995). Thus, other methods have recently been introduced for the correlation of Cretaceous nonmarine sediments; for examples by using other fossil groups such as fish (Yabumoto, 1994) and sedimentary facies suites (Sakai *et al.*, 1992; Seo *et al.*, 1992, 1994). One potential approach is to use the ostracode fossils that are abundantly found in Early Cretaceous nonmarine sediments. Cao (1996) described fossil ostracodes from the Cretaceous in Japan and compared them with those in China. However, her correlation is still insufficient because she discussed faunal assemblages based on the samples from restricted localities. For estimating the stratigraphical significance of each species and genus, a more detailed study of ostracode biostratigraphy is necessary. Recently, Hayashi (1998) reported 74 ostracode species belonging to 17 or more genera from Cretaceous nonmarine sediments. This study aims to establish a biozonation by using fossil ostracodes from the Lower Cretaceous Wakino Subgroup in North Kyushu and to

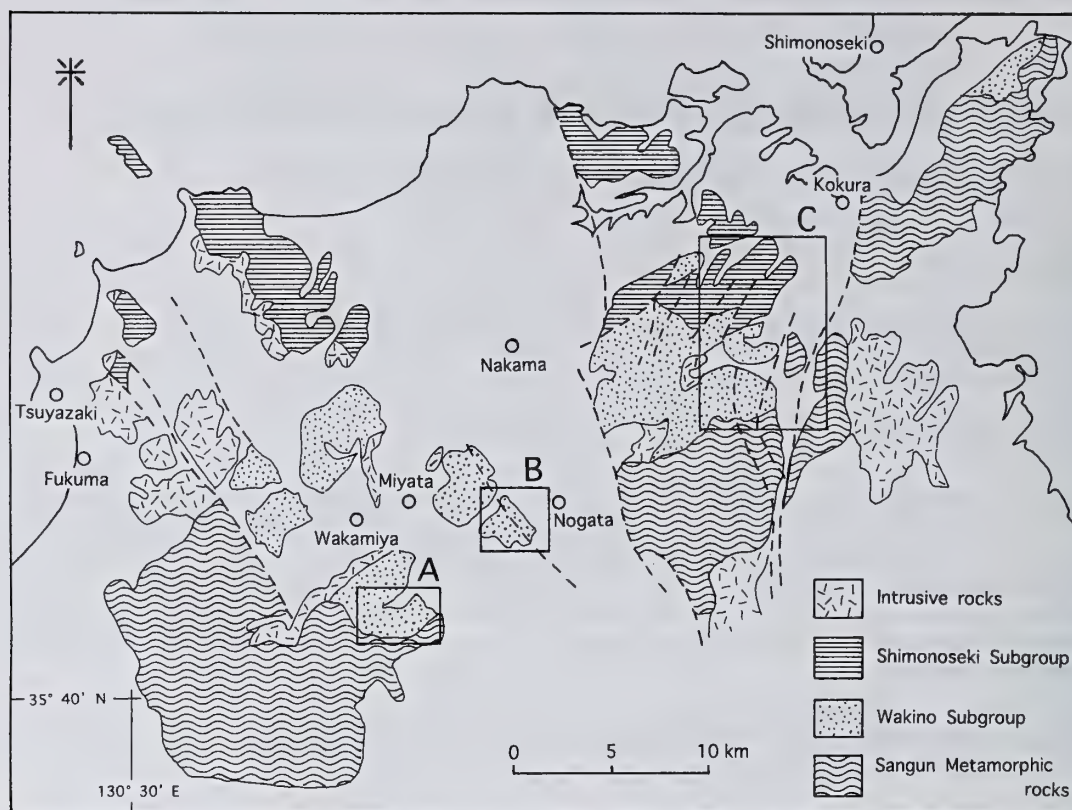
propose a correlation scheme.

### Geologic settings

Geologic settings of the study area were already reported in Hayashi (1998). Only the outlines of the geology are described here to the extent necessary for later description and discussion in this paper. Early Cretaceous nonmarine sediments are scattered in the Inner Zone of Southwest Japan. Especially in northern Kyushu and western Chugoku situated in the western areas of the Zone, they are assigned as the Kanmon Group (Matsumoto, 1951). The group is composed of the Wakino Subgroup in the lower part and the Shimonoseki Subgroup in the upper part. The Shimonoseki Subgroup overlies disconformably the Wakino Subgroup and oversteps the older basement in places.

In northern Kyushu, the group is distributed in two major areas (Figure 1). To the west of Nakama and Nogata cities, the upper part is generally observed sequentially from south to north, though it is discontinuously crop out into several isolated areas by some folding and faulting; to the east of Nakama and Nogata cities, obscure upper sequences are seen from south to north, but it is divided into many isolated blocks by much folding and faulting; hence the stratigraphic positioning of these delimited exposures is difficult.

Among many areas occupied by the Wakino Subgroup in Figure 1, three areas, i. e. Wakino, Yurino and southern Kokura areas, were selected for this study, because ostracode fossils have been known to occur only in these areas. As the Wakino and Yurino areas are relatively close to each other, those two are described together.



**Figure 1.** Geological map showing the distribution of the Kanmon Group in northern Kyushu (modified from Seo *et al.*, 1992). A: Wakino area, B: Yurino area, C: southern Kokura area.

Area	Wakino area			Yurino area	Southern Kokura area		
Reference	Kobayashi & I. Ota (1936)	Ota (1953)	Hase (1958, 1960)	Ota (1960)	Hase (1958, 1960)	Ota (1955, 1957, 1960)	Ota <i>et al</i> (1979)
Wakino Subgroup	Miyata shale	Upper Wakamiya Fm.	Upper Wakamiya Fm.		Equivalent of the Upper Wakamiya Fm.	Uppermost Fm. =W4	The Fourth Fm.
	Kinsho sandstone	Lower Wakamiya Fm.	Lower Wakamiya Fm.	W3	Equivalent of the Lower Wakamiya Fm.	Upper Fm. =W3	The Third Fm.
	Sengoku conglomerate	Nyoraida Fm.	Nyoraida Fm.	W2	Equivalent of the Nyoraida Fm.	Middle Fm. =W2	The Second Fm.
	Wakino Fm.	Sengoku Fm.	Sengoku Fm.	W1	Equivalent of the Sengoku Fm.	Lower Fm. =W1	The First Fm.

**Figure 2.** Comparison of stratigraphy of the Wakino Subgroup by previous studies.



### Wakino-Yurino area

In North Kyushu, the stratigraphical study of Mesozoic nonmarine strata was started by Kobayashi and Ota (1936) (Figure 2). They divided nonmarine strata of the Wakino area into the Wakino Formation and the unconformably overlying Sengoku conglomerate, Kinsho sandstone and Miyata shale in ascending order. Ota (1953), later, proposed the present stratigraphy consisting of the Sengoku, Nyoraida, Lower Wakamiya and Upper Wakamiya Formations in ascending order. This division in the Wakino area was supported by Hase (1958, 1960), and has been the standard stratigraphy of the Wakino Subgroup in northern Kyushu and western Chugoku.

The Wakino area, the type area of the Wakino Subgroup, is situated in the southernmost part of the areas occupied by the Kanmon Group (Figure 1). Successions ranging from the Sengoku to Nyoraida Formations are observed from south to north (Figure 3). The Sengoku Formation begins with the basal conglomerate that clinounconformably overlies the Sangun Metamorphic rocks (Figure 1). The basal facies are interpreted as a deposit dominated by debris flows by Okada *et al.* (1991). The middle and upper parts of the formation are made up of laminated or massive black mudstone, massive sandstone and pebble conglomerate, with intercalations of acidic tuff. They are considered to be a mixture of shallow-water, deltaic and lacustrine deposits. The Nyoraida Formation consists of rhythmic argillite intercalated with sandstone and granule to pebble conglomerate. These sediments are tuffaceous, and many of them show graded bedding. The argillite sediments are considered to have been deposited in deep-water lacustrine environments. The coarse-grained sediments are referred to as turbidite or

debris flow deposits (Seo *et al.*, 1992).

The Yurino area is situated 7 km northeast of the Wakino area. The geology of the area was mainly studied by Hase (1958, 1960). He considered that the equivalents of the Sengoku, Nyoraida and Lower Wakamiya Formations are distributed northeastward. These formations were assigned to W1, W2 and W3 formations respectively by Ota (1960). The lowermost strata in the Yurino area are, however, regarded as the Nyoraida Formation by Hayashi (1998). An upper sequence which is not found in the Wakino area is distributed in the Yurino area (Figure 4). The Lower Wakamiya Formation is composed of laminated or massive black mudstone intercalated with poorly sorted reddish sandstone and conglomerate. The Lower and Upper Wakamiya Formations are lithologically somewhat similar to each other. The former is, however, more frequently intercalated with discontinuous layers of pebble conglomerate. The Lower Wakamiya Formation shows various sedimentary structures and yields fossils indicative of very shallow water and desiccated terrestrial environments at some horizons. The occurrence of estherids indicates that the formation was deposited in very shallow water (Kusumi, 1979). The Upper Wakamiya Formation is composed of laminated or massive black mudstone intercalated with acidic tuff, sandstone and conglomerate. The formation shows various sedimentary structures and contains fossils indicative of shallow-water environments. The abundance of ostracodes indicates that the formation was deposited in a shallow-water environment.

### Southern Kokura area

Previous stratigraphical studies in this area were reviewed

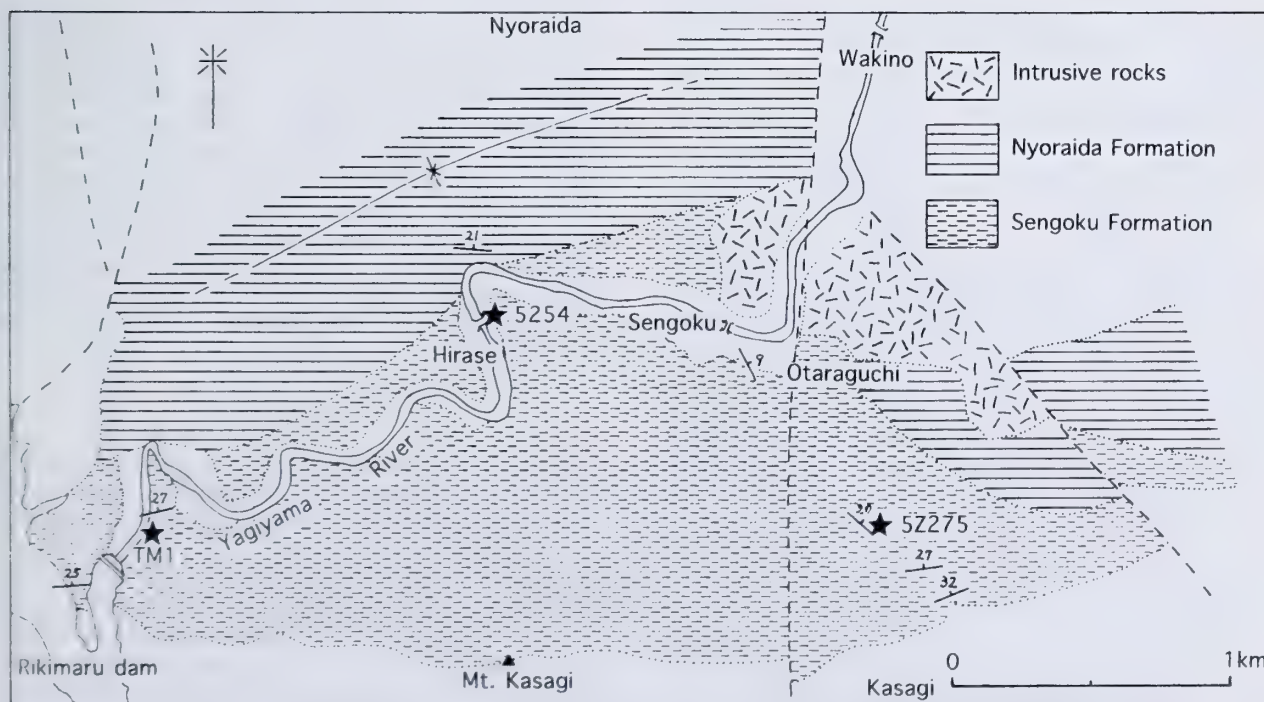


Figure 3. Geological sketch map and sampling localities of the Wakino Subgroup in the Wakino area (after Hayashi, 1998).

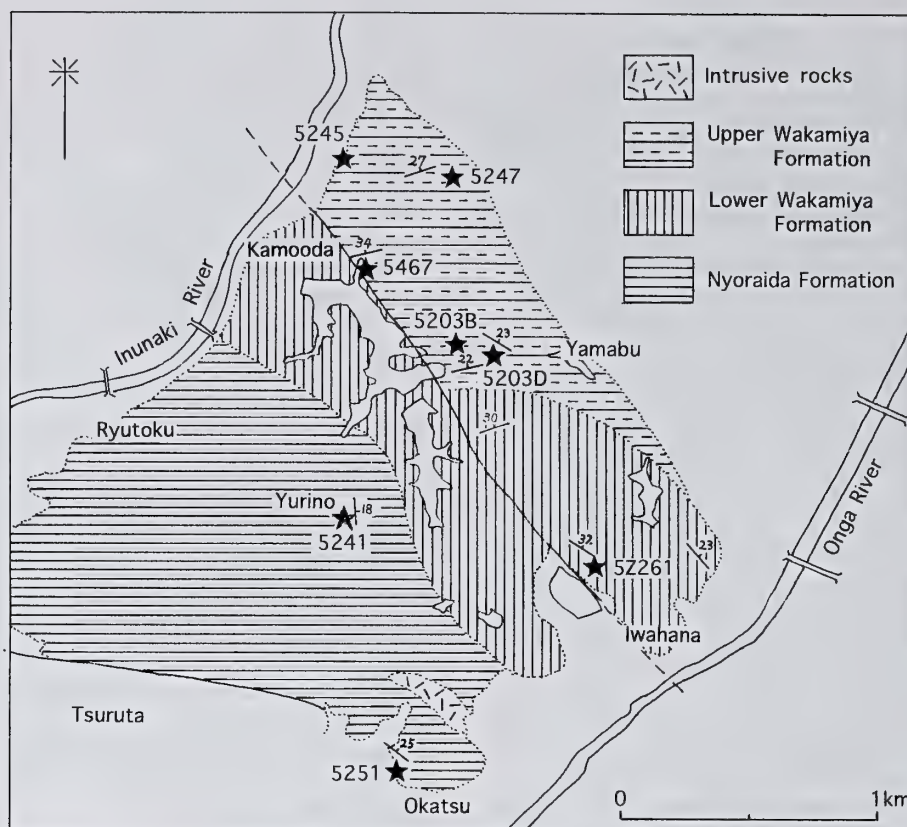


Figure 4. Geological sketch map and sampling localities of the Wakino Subgroup in the Yurino area (after Hayashi, 1998).

by Hayashi (1998). Ota (1955) revealed that the Wakino Subgroup of the southernmost area (Dobaru district) is composed of Lower, Middle and Upper formations in ascending order (Figure 2). Ota (1957) later added the Uppermost Formation to these three formations based on studies in the northern areas. Ota (1960) correlated these formations with the formations of other areas in the northern Kyushu and western Chugoku regions, and named them W1, W2, W3 and W4 formations. This division in the southern Kokura area was supported by Hase (1958, 1960), though he called them the equivalents of the Sengoku, Nyoraida, Lower Wakamiya and Upper Wakamiya formations, respectively. On the other hand, Ota *et al.* (1979) adopted the First, Second, Third and Fourth formations as the names of these formations, according to Matsushita (1968). This idiosyncratic nomenclature is presumably due to difficulties in lithological correlation over a wide area. The main reason for such variability of the stratigraphical units is that the lithology of the Wakino Subgroup is changeable laterally except for that of the Nyoraida Formation. In this paper, following Matsumoto (1962), the W1, W2, W3 and W4 formations of Ota (1960) are adopted for the subdivisions in the southern Kokura area.

The southern Kokura area is subdivided into several districts. In the southernmost part of the southern Kokura area, Dobaru district, W1 and W2 formations are distributed with a northward dip of the strata (Figures 5, 8). In other

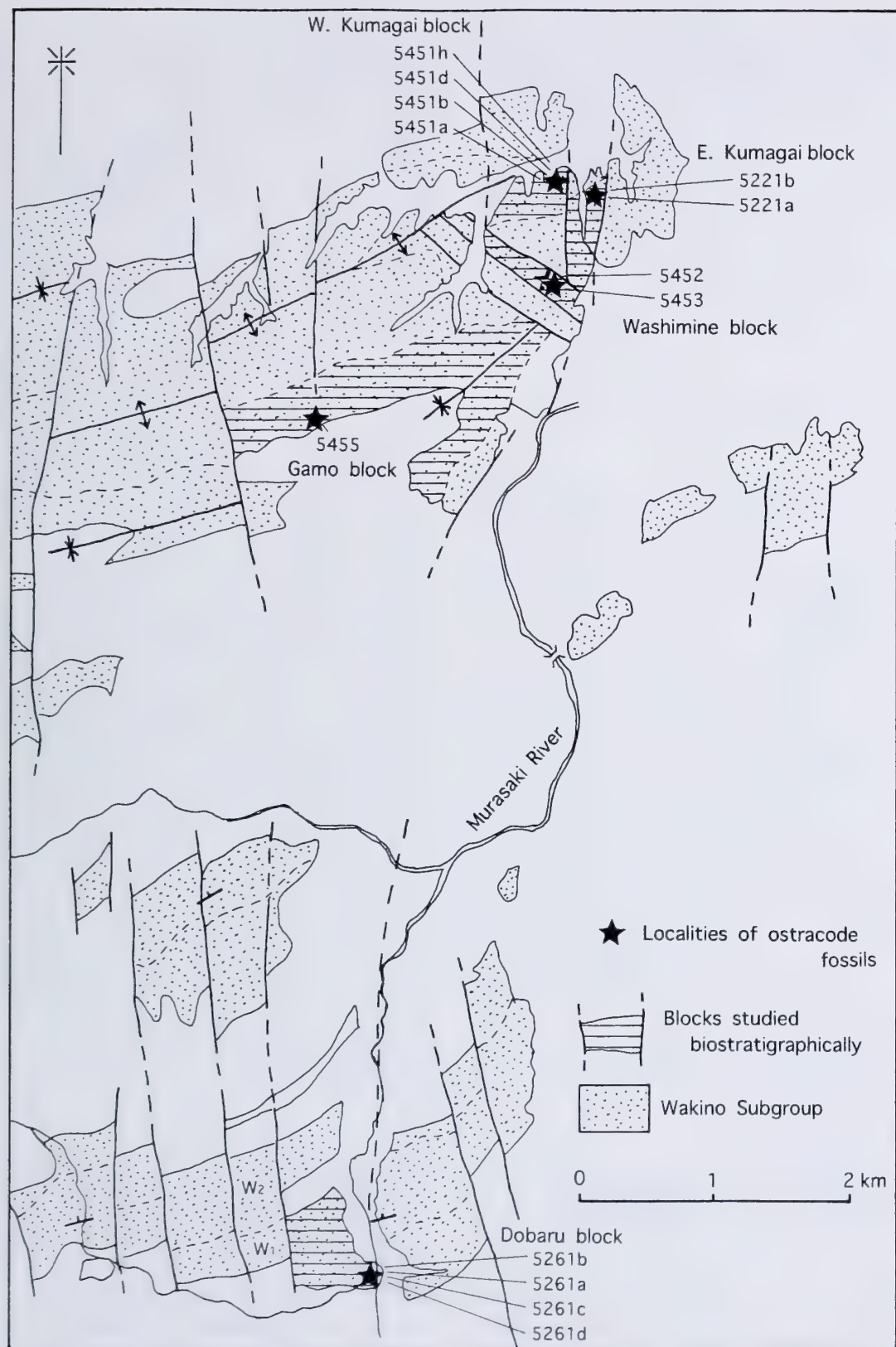
districts, however, the strata of the Wakino Subgroup are there in many faulted blocks and have suffered deformation by folding on various scales. Hence, the stratigraphical position of many blocks remains undetermined, though all of them are assigned to formations by previous studies (Ota, 1955, 1957, 1960; Hase, 1958; Ota *et al.*, 1979). In this study, the stratigraphical positions of five blocks, the Dobaru, Gamo, Washimine, East Kumagai and West Kumagai blocks, are reexamined and determined by using the ostracode zonation. With respect to the geological structure, this paper follows Hayashi (1998), who adopted the interpretations of Ota (1957) and Sakai *et al.* (1992) (Figure 5).

#### Method of study

All the forms of ostracode fossils in this paper were already described briefly by Hayashi (1998). Systematic descriptions and discussions on each species should be looked for there.

In this paper, first, ostracodes from each locality are referred to as assemblages based on dominant, subdominant, common and characteristic species and genus and on species association. However, the exact recognition of assemblages is difficult due to the small numbers of specimens, and some assemblages are gathered to establish one "assemblage zone" based on the similarity of their general





**Figure 5.** Geological sketch map and sampling localities of the Wakino Subgroup in the southern Kokura area (modified from Hayashi, 1998).

features. The reasoning of this method is that the fairly large variation in the ostracode faunas was presumably caused by a transportation mechanism of ostracode eggs in the Early Cretaceous which was different from that in the Recent. Krömmelbein (1962) pointed out that living non-marine ostracodes are occasionally transported a long distance by birds in mud sticking to feet and feathers.

With this method, an ostracode zonation has been successfully established in the Wakino Subgroup of the Wakino-Yurino area, northern Kyushu. Paleoenvironments of the ostracode assemblages are also discussed on the basis of other fossils and sedimentary structures.

Based on the ostracode zonation, the Wakino Subgroup in several blocks of the southern Kokura area is correlated to the level of formation with the Wakino Subgroup in the Wakino-Yurino area.

### Analysis of fossil ostracode assemblages

#### Occurrence

Ostracodes occur in the Sengoku, Nyoraida, Lower Wakamiya and Upper Wakamiya Formations in the Wakino-Yurino area, where 11 localities lie. In the southern Kokura area, ostracodes are found at 13 localities in five blocks, each of which consists of one or two units of those W1 to W4 formations distinguished by Ota (1960). These localities are shown in Figures 3-5, and their stratigraphic positions are shown in Figure 8.

Ostracode fossils occur almost always in mudstone or sandy mudstone. The mudstone of the Sengoku (W1) Formation, which is variable in lithology, contains poorly preserved fossil ostracodes at many horizons. The mudstone of the Nyoraida (W2) Formation, however, scarcely yields fossil ostracodes. The scarcity is explained by the fact that the mudstone is interbedded with graded sandstone of turbidite origin. The mudstone of the Lower Wakamiya (W3) Formation, which is intercalated with poorly sorted discontinuous sandstone layers, also yields few ostracodes in the Wakino-Yurino area, but does so abundantly in the southern Kokura area. Such a regional scarcity is presumably due to the dominance of terrestrial fluvial plain environments. In contrast, the mudstone of the Upper Wakamiya (W4) Formation, which is thinly well-stratified and intercalated with sorted sandstone layers from horizon to horizon, contains abundant and varied fossil ostracodes. This may be related to widespread shallow-water environments during deposition of the formation.

#### Ostracode assemblages

Twelve ostracode assemblages have been identified in the Wakino Subgroup in the study area: five in the Wakino-Yurino area and seven in the southern Kokura area. Each of the ostracode assemblages is described below.

##### Wakino-Yurino area

One ostracode assemblage has been identified from the Sengoku Formation in the Wakino area, and five assemblages from the Nyoraida, Lower Wakamiya and Upper Wakamiya Formations in the Yurino area (Figures 6, 8).

##### 1. *Darwinula* assemblage

In the Sengoku Formation of the Wakino area and the Nyoraida Formation of the Yurino area, the ostracode assemblages at all the localities are commonly characterized by the abundant occurrence of species belonging to the genus *Darwinula*. This assemblage, named the *Darwinula* assemblage, is variable in generic composition. In the lower Sengoku and upper Nyoraida Formations, it contains the genus *Damonella* which is here represented by a single species, *D. cf. obata*. The species is especially abundant in the lower Sengoku Formation. The genus *Clinocypris*, comprising one or two species, is present in the assemblage at some localities. *Damonella* and *Clinocypris* are characteristic genera of the *Darwinula* assemblage, but they are not always common at all the localities. The genus *Cypricerus*, represented by a single species, seems to be another characteristic genus, but it is obtained from only one locality. It is noticeable that the assemblage is characterized by the entire absence of the genus *Cypridea*, which is a dominant or common genus in all the other assemblages.

The dominant genus *Darwinula* comprises different species at different localities. For example, this component is composed exclusively of *D. incruva* at Locs. TM1 and 5251, and *D. submuricata* in Loc. 5254, and *D. cf. giganimpudica*, *D. postitruncata* and *D. sp.1* at Loc. 52275, and consists of *D. cf. oblonga* and other new species at Loc. 5241. The subordinate genus *Clinocypris* also comprises different species at different localities. Namely, it is represented by *C. obliquetruncata* at Loc. TM1, and *C.?* sp. 2 and *C.?* sp. 4 at Loc. 5251. *Damonella cf. obatai* occurs closely together in abundance, especially forming "ostracode layers" in the black mudstone at Loc. 52275.

##### 2. *Cypridea?* cf. *renalata* subassemblage

At Loc. 52261, where is exposed the middle part of the Lower Wakamiya Formation, only one assemblage from that formation is defined. In this paper, an assemblage which is found at only one locality is dealt with as a subassemblage (written as S.A.), because it may represent only one part of the indicated assemblage. The subassemblage is taxonomically monotonous with a small number of individuals. The dominant species is small-sized *Cypridea?* cf. *renalata*, which is also characteristic of the subassemblage. It makes up about 70% or more of the total ostracode specimens of the subassemblage, in spite of sporadic occurrence. The subordinate species are *Cypridea* sp. 4, *Mongolianella cf. zerussata longiuscula*, *M. aff. zerussata longiuscula* and *Rhinocypris? cf. jurassica*, all of which are small in size and rare.

##### 3. *Mongolianella*-*Cypridea* assemblage

This assemblage is recognized in the lower and upper parts of the Upper Wakamiya Formation.

At Locs. 5203D and 5203B of the Yurino area in the lower part of the Upper Wakamiya Formation, the ostracode assemblage is characterized by many species of *Mongolianella* and *Cypridea*. Among them, *Mongolianella zerussata longiuscula*, *M. cf. palmosa*, *M. sp. 1*, *Cypridea tera*, *C. (C.) cf. delnovi* and *C. (Cyamocypris) sp.1* possess a large-sized carapace, and are not found in the underlying formations (Figure 9). Medium-sized *Cypridea* such as *C. kyushuensis* and *C. (Pseudocypridina) aff. jianchangensis*



● >10   ● >3   ● >1

**Figure 6.** Ostracode species, assemblages and biostratigraphical zonation in the Wakino-Yurino area.

are also common or abundant in the assemblage. *Eoparacypris* and *Candona* appear for the first time in this assemblage. Almost all the species of this assemblage have not been found in the underlying assemblages. Among them are "*Rhinocypris* sp. 2" of Cao (1996) with three very large laterally located nodules and *Eoparacypris macroselina* with a characteristic elongate-triangular carapace in lateral view. Consequently, this assemblage is quite different from the *Darwinula* assemblage and the *Cypridea*? *renalata* subassemblage.

In the upper part of the Upper Wakamiya Formation at Loc. 5247 of the Yurino area, the ostracode assemblage is dominated by *Cypridea* (*Pseudocypridina*) *globra* and subdominated by *Mongolocypis* sp. 1. Other species, *Cypridea* (C.) cf. *delnovi* and *Mongolianella* cf. *palmosa*, are rare in occurrence; their number of specimens are less than 20% of the total number of individuals. It is almost the same as the above-mentioned assemblage in the lower part of the same formation, with little differences in species composition. This assemblage shows a lower species diversity ( $\lambda = \sum Xi (Xi - 1) / N(N - 1) = 0.44$ ) than the assemblage at Locs. 5203D ( $\lambda = 0.15$ ) and 5203B ( $\lambda = 0.18$ ).

#### 4. *Cypridea tera* subassemblage

In the middle part of the Upper Wakamiya Formation at Loc. 5467 of the Yurino area, a small number of fossil ostracodes occurs sporadically in mudstone. The ostracode assemblage is dominated by *Cypridea tera* and subdominated by *Cypridea* (*Pseudocypridina*) aff. *jianchangensis*. "*Cypridea* sp. 2" of Cao (1996) is also rarely associated in it. This species association is referred to as a subassemblage, because they come from a single locality. This subassemblage is here named after the most dominant *C. tera*.

The subassemblage is thought to be closely related to the *Mongolianella-Cypridea* assemblage, because of the dominance of the characteristic species of the *Mongolianella-Cypridea* assemblage.

#### 5. *Eoparacypris* subassemblage

In the uppermost part of the Upper Wakamiya Formation at Loc. 5245 of the Yurino area, the ostracode assemblage is dominated by the genus *Eoparacypris*. This is also assigned to a subassemblage, owing to the occurrence at a single locality. The genus *Eoparacypris* in this subassemblage consists of *E.* cf. *attenuata* and *E. macroselina*. Other genera such as *Cypridea* and *Darwinula* are included in the assemblage, but they are less than 20% of the total number. Therefore, this assemblage is characterized by low species diversity ( $\lambda = 0.41$ ).

The genus *Eoparacypris* is found only in the *Mongolianella-Cypridea* assemblage other than in this subassemblage. The subordinate species are *Cypridea kyushuensis* and *Darwinula contracta*, the former is also included in the *Mongolianella-Cypridea* assemblage at both Locs. 5203D and 5203B, and the latter in the same assemblage at Loc. 5203B. Therefore, the *Eoparacypris* subassemblage shows a close affinity to the *Mongolianella-Cypridea* assemblage.

### Southern Kokura area

Seven ostracode assemblages have been identified in the

Wakino Subgroup in five blocks of the southern Kokura area (Figures 7, 8). One assemblage was identified in each of the Dobaru and Gamo blocks, and the Washimine and East Kumagai blocks together. Four other assemblages were identified from the West Kumagai block. They are described as follows.

#### 6. *Cypridea-Darwinula* assemblage

Dark gray sandy mudstone overlying unconformably the Sangun Metamorphic Rocks at Locs. 5261d, 5261c, 5261a and 5261b in the Dobaru block of the southern Kokura area is undoubtedly assigned to the W1 formation. These localities are situated closely together within a stratigraphical interval of only 5.3 m. As shown in Figure 7, the ostracode assemblages from this mudstone appear to be different in species composition at different horizons. This, however, is due to differences in individual numbers at respective localities; relatively large numbers of individuals and species were collected from Locs. 5261c and 5261b, relatively small numbers from Locs. 5261d and 5261a. Consequently, the ostracode assemblage is better represented at Locs. 5261c and 5261b. In spite of these differences, *Cypridea*? sp. 3 is common among samples from the four localities. Therefore, the species from these four localities are considered to form together a single assemblage.

This assemblage is characterized by species of the genera *Cypridea* and *Darwinula* with six and three species, respectively. *Clinocypris* is a common genus in the assemblage, with one certain and three uncertain species. The genus *Mongolianella* is also common in the assemblage.

All the six species of *Cypridea*, except for *C. (C.)* cf. *tuberculostrata*, are confined to this assemblage. These are interpreted to be older forms of *Cypridea* than those in the Wakino-Yurino area. Thus, they are probably contemporary with the *Darwinula* assemblage. The occurrence of the subgenus *Cypridea* (*Cyamocypris*) should be noted, because according to Cao (1996), the species of the subgenus lived in very limited environments in China. A few individuals of *C. (C.)* cf. *oblonga*, however, were obtained here. This scarcity may imply that this locality was in relatively open environments.

As to the genus *Darwinula*, relatively large forms such as *D. cf. leguminella* are dominant, but any species is not stratigraphically significant. They are significant, however, as indices of paleoclimate (Ye, 1994).

*Damonella* cf. *ovata*, one of the characteristic species of the *Darwinula* assemblage in the Wakino-Yurino area, is included in this assemblage.

#### 7. *Cypridea tera* subassemblage

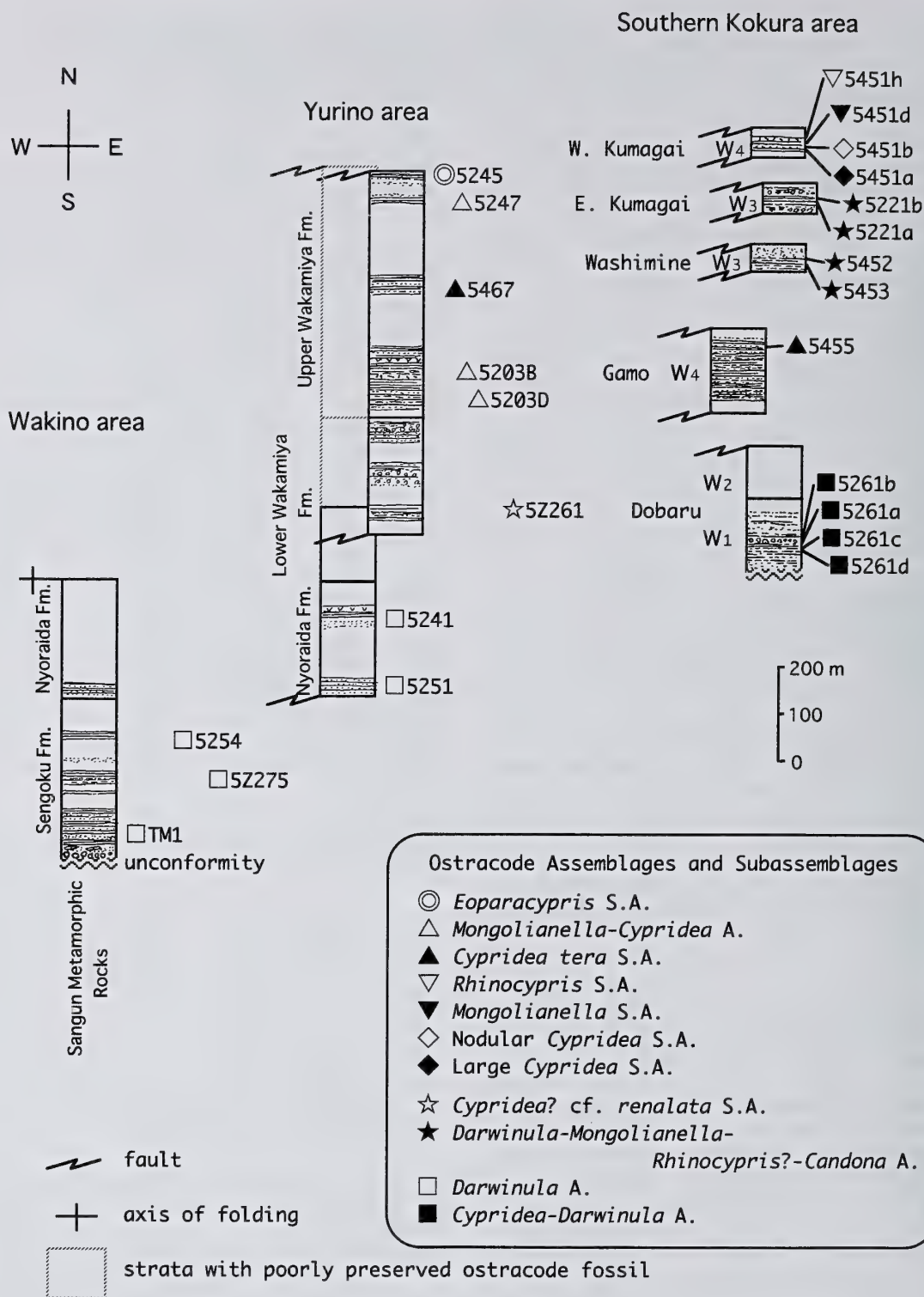
The ostracode assemblage from Loc. 5455 in the Gamo block is characterized by the abundance of *Cypridea tera*, accompanied by *Cypridea* (*Pseudocypridina*) aff. *jianchangensis* and *C. cf. anhuaensis*. It is almost the same as that from the Upper Wakamiya Formation at Loc. 5467 of the Wakino-Yurino area.

The subassemblage has a relation to the *Mongolianella-Cypridea* assemblage, because two of the three dominant and subordinate species are also found commonly in the *Mongolianella-Cypridea* assemblage.



Block of Southern Kokura area		Dobaru		Gamo	Washimine	E. Kumagai	W. Kumagai
Formation	Loc.	W1	W2	W4	W3	W3	W4
Species	Loc.	5261d -c -a -b		5455	5453 5452	5221a -b	5451a -b -d -h
<i>Cyprinotus toutaiensis</i>						•	
<i>Eucypris</i> ? sp.1						•	
<i>Lycocypris</i> cf. <i>sinuolata</i>			•			•	
<i>Mongolianella zerussata longiuscula</i>							•
<i>M.</i> cf. <i>zerussata longiuscula</i>		•	•				
<i>M.</i> aff. <i>zerussata longiuscula</i>						•	
<i>Mongolianella</i> aff. <i>palmosa</i>						•	
<i>Mongolianella</i> cf. <i>palmosa</i>							•
<i>Mongolianella</i> ? sp.2					•		•
<i>Mongolianella</i> ? sp.3					•	•	
<i>Mantelliana jingguensis</i>		•					
<i>Mantelliana</i> ? sp.1						•	
<i>Sinocypris</i> cf. <i>jinghongensis</i>						•	
<i>Candona praevara</i>					•	•	
" <i>Candona</i> sp. 4" PAIK ET AL.						•	
<i>Cyclocypris</i> ? cf. <i>valida</i>						•	
<i>Cyclocypris</i> ? sp. 1			•				
<i>Damonella</i> cf. <i>ovata</i>			•				
<i>Rhinocypris</i> cf. <i>tuberculata</i>							•
" <i>Rhinocypris</i> cf. <i>jurassica</i> j." CAO							•
<i>Rhinocypris</i> ? cf. <i>jurassica</i>						•	•
<i>Rhinocypris</i> ? aff. <i>jurassica</i>	•					•	•
" <i>Rhinocypris</i> sp.1" CAO						•	•
" <i>Rhinocypris</i> sp.2" CAO							•
<i>Cypridea</i> (C.) cf. <i>actuosa</i>	•	•	•				
<i>Cypridea</i> (C.) cf. <i>tuberculostrata</i>	•	•				•	
<i>Cypridea</i> (C.) aff. <i>delnovi</i>						•	•
" <i>Cypridea</i> (C.) sp.4" PAIK ET AL.							•
<i>Cypridea</i> ( <i>Cyamocypris</i> ) cf. <i>oblonga</i>		•					
<i>C.</i> ( <i>Pseudocypridea</i> ) <i>jinjuria</i>					•		
<i>C.</i> (P.) <i>jianchangensis</i>	•	•	•				
<i>C.</i> (P.) aff. <i>jianchangensis</i>				•			
<i>Cypridea</i> cf. <i>anhuaensis</i>				•			
<i>Cypridea</i> <i>kyushuensis</i>				•		•	
<i>Cypridea</i> <i>tera</i>				•			
<i>Cypridea</i> ? sp.1		•	•				
<i>Cypridea</i> ? sp.3	•	•	•				
<i>Cypridea</i> sp.5							•
<i>Clinocypris</i> sp.1			•				
<i>Clinocypris</i> ? sp.2			•				
<i>Clinocypris</i> ? sp.3			•				
<i>Clinocypris</i> ? sp.4			•				
<i>Darwinula contracta</i>							•
<i>Darwinula incurva</i>				•			
<i>Darwinula</i> cf. <i>jonesi</i>			•				
<i>Darwinula</i> cf. <i>leguminella</i>	•	•	•		•	•	
<i>Darwinula</i> cf. <i>submuricata</i>			•				
<i>Darwinula</i> cf. <i>sarytirmensis</i>						•	
<i>Darwinula</i> aff. <i>subparallela</i>					•	•	
Assemblage & Subassemblage		<i>Cypridea</i> - <i>Darwinula</i> A.		<i>Cypridea</i> <i>tera</i> S.A.	<i>Darwinula</i> - <i>Mongolianella</i> - <i>Rhinocypris</i> ?- <i>Candona</i> A.	Large <i>Cypridea</i> S.A. Nodular <i>Cypridea</i> S.A. <i>Mongolianella</i> S.A. <i>Rhinocypris</i> S.A.	

Figure 7. Ostracode species and assemblages in five blocks in the southern Kokura area. The formations in Gamo, Washimine, East Kumagai and West Kumagai blocks are respectively inferred from their ostracode assemblages.



**Figure 8.** Stratigraphical distribution of ostracode assemblages. The relationships between assemblages and biostratigraphical zones are shown in Figure 6.



#### 8. *Darwinula-Mongolianella-Rhinocypris*?-*Candona* assemblage

From Locs. 5221a and 5221b in the East Kumagai block, the former located 7 m below the latter, a high-diversity ( $\lambda = 0.11-0.24$ ) ostracode assemblage was obtained. The assemblage involves 19 species belonging to 11 genera. The faunal composition is the most complex among all the assemblages described in this paper. The sample size for the two dominant species, *Darwinula* aff. *subparallela* and *Rhinocypris*? cf. *jurassica*, are only slightly larger than those for several subordinate species. Therefore, it is inadequate to name the assemblage after the leading generic or species names. Among the subordinate species, four species belong to the genus *Mongolianella* and two species to the genus *Candona*. Thus, the high-diversity assemblage is named the *Darwinula-Mongolianella-Rhinocypris*?-*Candona* assemblage.

The assemblage is somewhat similar to the *Cypridea-Darwinula* assemblage and *Darwinula* assemblage in the abundance of *Darwinula*, and also resembles the *Mongolianella-Cypridea* assemblage in the abundance of *Mongolianella*. This may mean that the assemblage is transitional from early *Darwinula*-dominant assemblages to later large Cypridacean-abundant assemblages.

At species level, however, the components of the genus *Darwinula* in this assemblage are different from those of the *Darwinula* assemblage of the Sengoku and Nyoraida Formations and the *Cypridea-Darwinula* assemblage of the Dobaru block, except for *D.* cf. *leguminella* with a long stratigraphical range extending throughout the Wakino Subgroup. Two of the three species of the genus *Cypridea* are held in common the *Cypridea-Darwinula* assemblage in the Upper Wakamiya Formation in the Yurino area, and the remaining one is common with the assemblage of the Dobaru block.

The assemblages at Locs. 5453 and 5452, the former 10 m below the latter are also identified with the *Darwinula-Mongolianella-Rhinocypris*?-*Candona* assemblage. This identification is based on the abundance of *Darwinula* and *Mongolianella*, and on the fact that four of the seven species comprising the assemblage also occur in the high-diversity assemblage of the East Kumagai block. In particular, three of the four species characteristically occur in the East Kumagai block.

#### 9. Large *Cypridea* subassemblage

At Loc. 5451a of the West Kumagai block, a very large *Cypridea*, *C.* sp.5, occurs exclusively. This species is the biggest in all the ostracodes of the Wakino Subgroup. Other species are few and cannot be identified to species because of poor preservation. This unique assemblage seems to have settled in a limited environment on ash-field bottoms. This ostracode association is assigned to a subassemblage owing to its restriction to the limited occurrence at a single locality.

#### 10. Nodular *Cypridea* subassemblage

The characteristic *Cypridea* with nodulated surface, "*C.* sp. 4" of Paik *et al.* (1988), occurs dominantly at Loc. 5451b, which is about 3.8 m above Loc. 5451a within the same West Kumagai block. Such a nodulate species is very rare in the Wakino Subgroup, though another nodulate species is

present in the *Rhinocypris* subassemblage from the same West Kumagai block and the *Mongolianella-Cypridea* assemblage from the Upper Wakamiya Formation in the Yurino area. A subordinate species is large-sized *Mongolianella* cf. *palmosa*, which is characteristic of the Upper Wakamiya Formation in the Wakino-Yurino area. This association of ostracodes is also assigned to a subassemblage owing to its occurrence at a single locality.

#### 11. *Mongolianella* subassemblage

A quite different assemblage from that of Locs. 5451a and 5451b is found at 5451d about 1.5 m above Loc. 5451b. Because of small numbers of individuals, only one species was so far found at this locality. This exclusive species is *Mongolianella zerussata longiuscula*, which is, in contrast, coexistent with many other species at Loc. 5203B. This ostracode association is also assigned to a subassemblage owing to its appearing at a single locality.

#### 12. *Rhinocypris* subassemblage

This assemblage is found at Loc. 5451h, which is located 3.4 m above Loc. 5451d, and shows the highest diversity ( $\lambda = 0.21$ ) among the four localities within the West Kumagai block. It is named because of the abundance of *Rhinocypris*.

The genus *Rhinocypris* of this subassemblage consists of five species, *R.* cf. *tuberculata*, *R.*? cf. *jurassica*, "*R.* cf. *jurassica jurassica*", "*R.* sp.1" and "*R.* sp.2", among which the last three were described by Cao (1996). Of the three species, "*Rhinocypris* sp. 2" of Cao (1996) is common to the *Mongolianella-Cypridea* assemblage from the Upper Wakamiya Formation in the Yurino area. *Cypridea* (*C.*) aff. *delnovi* is also abundant in the subassemblage.

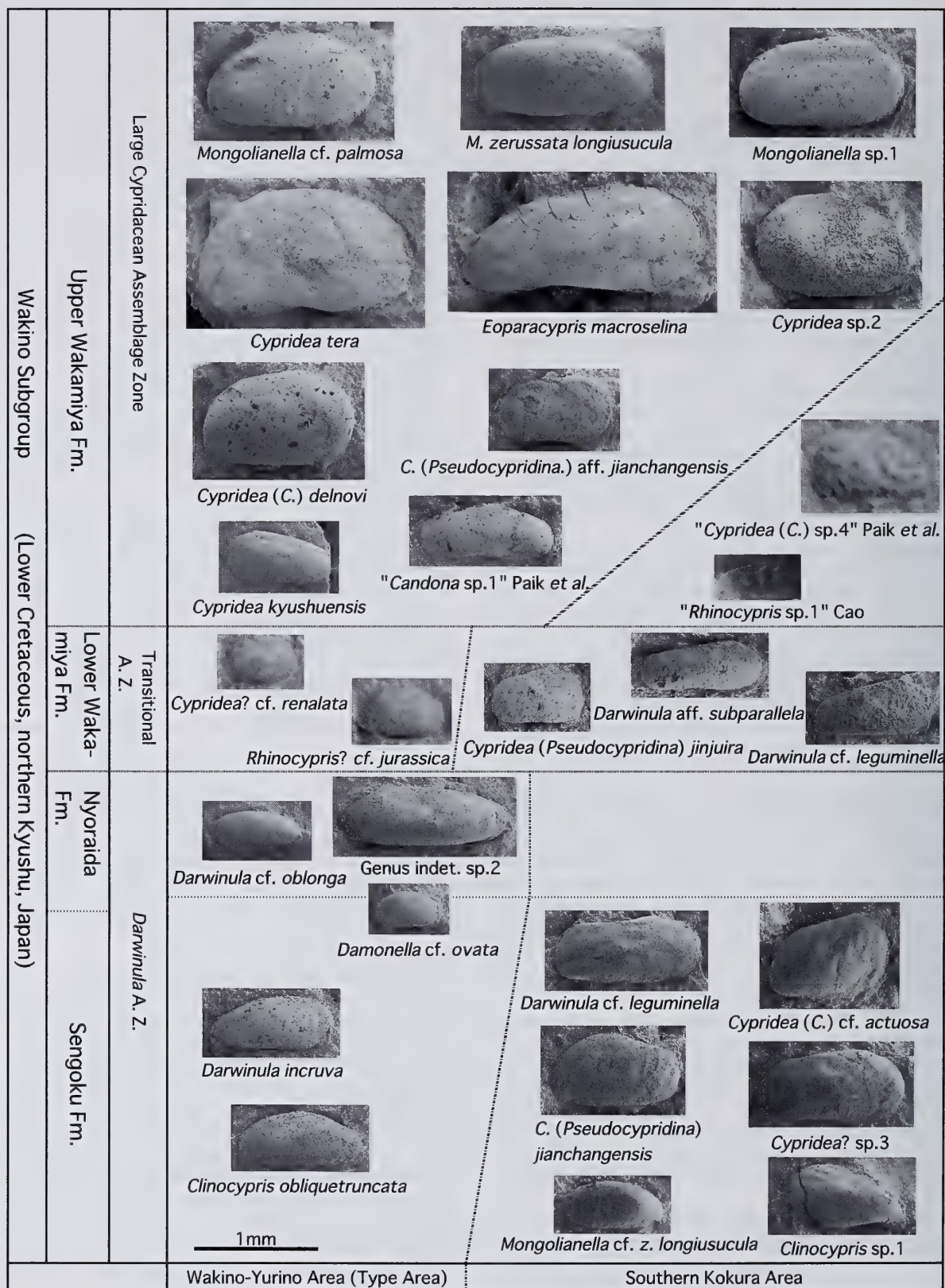
### Ostracode assemblages and sedimentary environments

Characteristics of Early Cretaceous ostracode assemblages.—Generally, the diversity of nonmarine ostracode assemblages from the Wakino Subgroup is extremely high as compared to those of Recent or Cenozoic ones. This high diversity is most remarkable in the Lower Cretaceous ostracode assemblages all over the world. However, the reasons behind this high diversity have not been sufficiently discussed until now, in spite of the importance for assessments of ostracode assemblages.

Some living ostracode assemblages from isolated lakes around the world are remarkably similar to one another. This owes much to transport by migratory water birds, either in mud sticking to their feet and trapped in feathers or in the intestinal tract (Krömmelbein, 1962; Brasier, 1980). Since most nonmarine ostracode eggs are very resistant against desiccation, their dispersion could be largely accomplished by water birds. However, such Early Cretaceous migratory water birds are unknown (Figure 10). The oldest evidence of water birds in East Asia is the footprints of webbed feet from the Upper Cretaceous Uhangri Formation of Korea (Yang *et al.*, 1995; Figure 10). The age of the formation is younger than 85-92 Ma (radiometric age of the Hwangsan Tuff in the underlying formation) and older than 63-67 Ma (radiometric age of the Haennam basin intrusives in the overlying formation).

On the other hand, shore birds had already become habi-





**Figure 9.** Some of the representative ostracodes from the Wakino Subgroup are arranged at their stratigraphical and geographical positions.



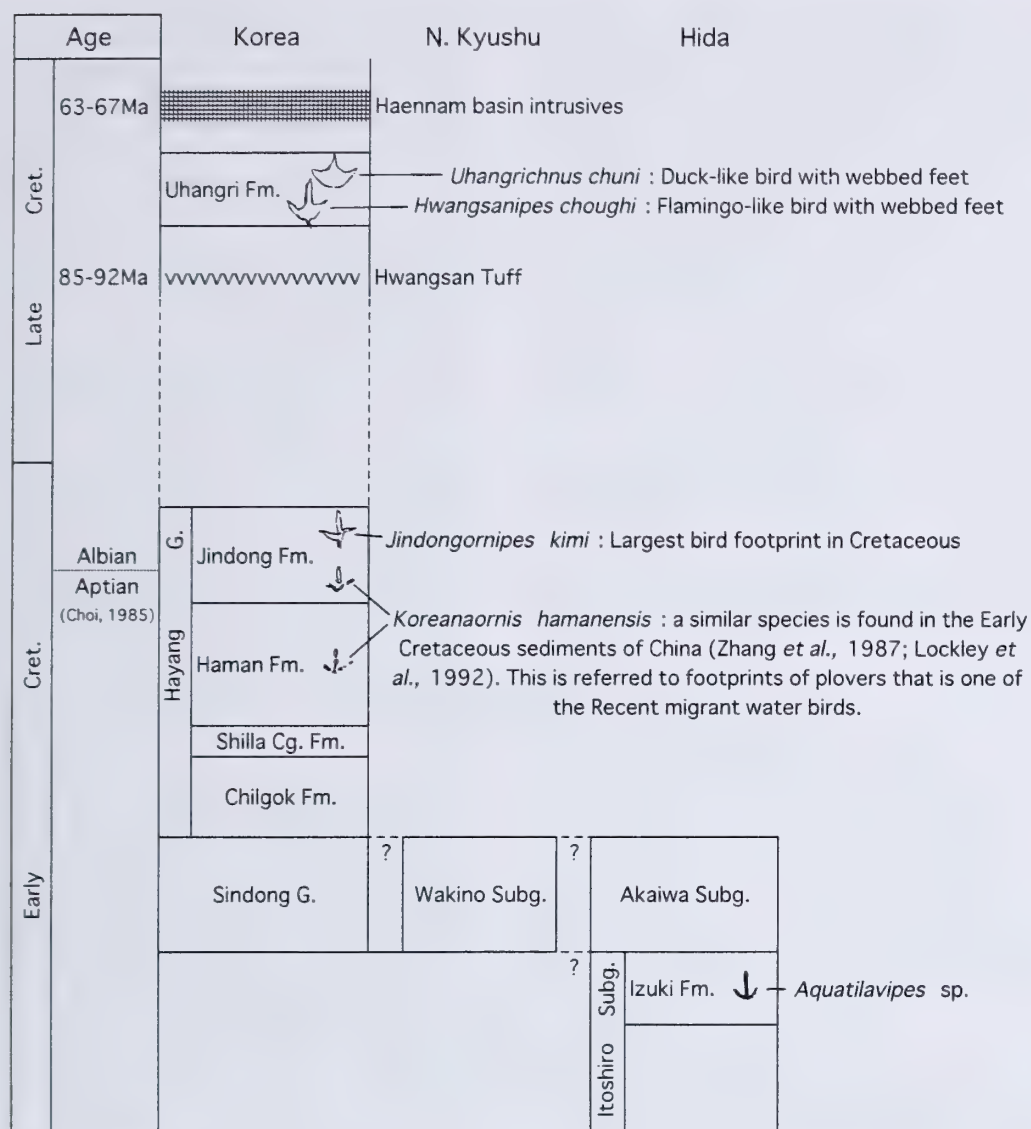


Figure 10. Occurrence of Cretaceous water and shore birds in Korea and Japan.

tants of lacustrine shorelines in East Asia by Early Cretaceous. For example, Kim (1969) reported avian tracks associated with many invertebrate trace fossils from the Haman Formation of the Lower Cretaceous Hayang Group of the Kyeongsang Supergroup in Korea. More recently Choi (1985) has suggested that these deposits are probably Aptian to early Albian in age. Yang *et al.* (1990) and Lockley *et al.* (1991) discovered many avian tracks at 31 localities in the Jindong Formation that overlies the Haman Formation. They concluded that there appear to be at least two quite distinct footprint types, *Jindongornipes kimi* and *Koreanaornis hamanensis* in the Jindong Formation. *Koreanaornis hamanensis* resembles the footprint of various modern species of plovers. Recent plovers are migratory shore birds, one of which is known to migrate several thousand kilometers. Matsukawa (1991) reported bird tracks

from the Valanginian-Hauterivian? Izuki Formation (upper part of the Itoshiro Subgroup of the Tetori Group) in central Japan, which is slightly older than or almost contemporaneous with the Wakino Subgroup.

Considering that aviform tracks are widespread and a significant component of Early Jurassic ichnological assemblages, birds presumably evolved rapidly in the Late Jurassic and Early Cretaceous (Lockley *et al.*, 1992). The shore bird radiation may have occurred in Early Cretaceous, but this apparently did not yet produce fully aquatic birds. Given this, it may be surmised that only shore birds were active on the shore of the sedimentary basin of the Early Cretaceous Wakino Subgroup. Consequently, the ostracodes whose eggs could then be transported by birds were restricted to shoreline-inhabiting species. It is considered that species living in water deeper than 10 cm or so

were seldom transported by birds. Therefore, many species presumably evolved in situ in each lake, giving rise to high-diversity assemblages. The similarity of contemporaneous ostracode assemblages within the same lakes may have been maintained. The similarity, however, was not warranted in assemblages of isolated lakes long distances apart in the Early Cretaceous. Namely, it is suspected that the ostracode assemblages were different from lake to lake.

As Lower Cretaceous ostracode assemblages were changeable from place to place, ostracode biostratigraphical zonation and correlation should not be based directly on ostracode assemblages of a certain kind, but on more general features common among closely related assemblages.

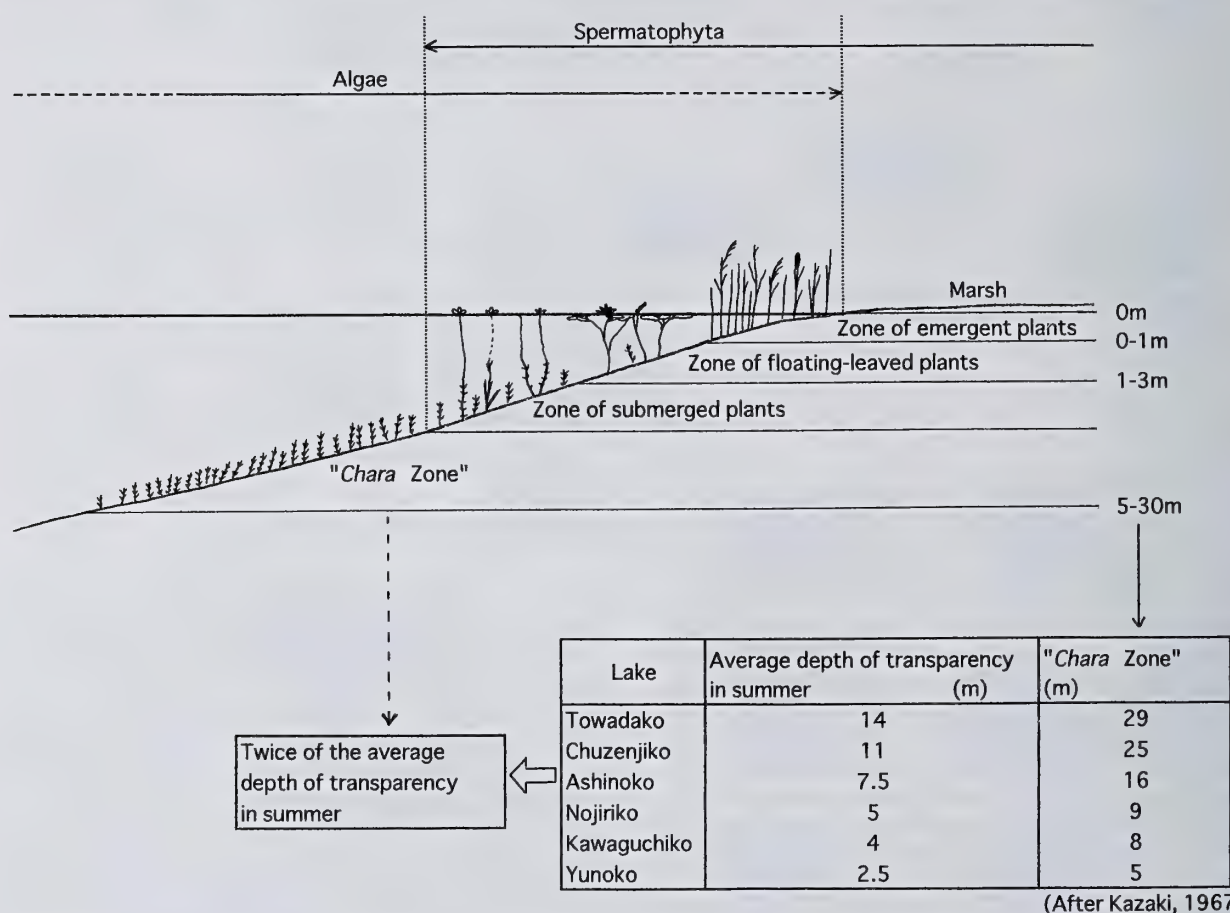
Sedimentary environments indicated by fossil charophytes and estherids.—At some horizons of the Wakino Subgroup, fossil charophytes are found abundantly together with ostracode fossils. Fossil estherids occur accompanying ostracode fossils at many horizons. These charophyte and estherid fossils are useful to assess sedimentary environments. Ecological discussions of these taxa have been little done, in spite of their importance for indications of paleoenvironments. Then, it should be discussed what kind

of environments these taxa indicate.

*Sedimentary environments indicated by fossil charophytes:* Fossil charophytes occur abundantly in the Sengoku Formation at Loc. TM1 of the Wakino area and the Upper Wakamiya Formation at Loc. 5247 of the Yurino area.

According to the classification generally accepted, charophytes consist of 3 orders and 6 families including fossil species. But of the three only one order (Charales) with four families survives today, of which only one family (Characeae) has living species. About 250 living species are known from all over the world, of which about 70 species are living in Japan.

This group appeared in the Silurian, and became highly diversified by the Cretaceous but declined to the Recent. The ecology of recent charophytes is very significant, because it forms "Chara zone" in the lowermost part of the depth distribution of aquatic plants in lakes (Kazaki, 1967; Figure 11). The depth of the lower limit of the "Chara zone" is inferred to be about twice the average depth of transparency in summer, based on the data shown in Figure 11. The upper limit of the "Chara zone" is determined by the depth of the overlying "zone of Submerged Plants", which ranges from one to



**Figure 11.** Schematic diagram showing vertical zonation of aquatic large plants in lake shore environments (partly adopted from Kazaki, 1967). Compiled from many ecological studies of recent freshwater botany. Vertical zonation is generally formed in the aquiferbosa, that is, a shallow bottom covered by aquatic plants. The lowermost part is exclusively abundant in charophytes, which form the "Chara zone".



several meters. Consequently, the Recent "Chara zone" is usually formed on the shallow bottom that is deeper than several meters and shallower than 30 m. In the Cretaceous, however, the upper limit of the zone is inferred to have been shallower than that in the Recent, because plants forming zones over the "Chara zone", most of which belong originally to terrestrial spermatophytes, invaded submerged environments from terrestrial environments during or after the Cretaceous. Therefore, the "Chara zone" is considered to have been a little wider, namely, a few to 30 m. If this is true, charophytes accompanied by many other aquatic plants indicate the "zone of the submerged plants", which is shallower than a few meters.

In such shallow water, a calm environment in which plants can grow is considered to have been restricted to enclosed margins of lakes or marshes on the fluvial plain, because waves and currents usually prevent plants from growing. Large aquatic plants tend to grow in bays rather than in open-shore environments (Ikushima, 1969). Among many kinds of aquapants, charophytes especially prefer lentic environments to lotic environments, as lentic environments favor the swimming of sperm during fertilization.

As discussed above, the abundant occurrence of fossil charophytes surely indicates shallow and calm water environments. Such environments can be seen in enclosed bottom parts of marginal lakes, shallow swamps or marshes on the fluvial plain.

*Sedimentary environments indicated by fossil estherids:* In the southern Kokura area, estherids were collected by Ota (1957) from W3 and W4 formations exposed near Yamada Park and were described as *Euestheria imamurai*, *E. kokuraensis* and *Cyclestheroides* sp. by Kusumi (1960). Additional estherids were collected by Ota *et al.* (1979) from W3 and W4 formations in the same place. Among them, those from the basal part of W4 formation were identified as *Euestheria imamurai*, *E. kokuraensis* and *Cyclestheroides* sp. by Kusumi (1979). In the Wakino-Yurino area, estherid fossils have been newly found in the Lower Wakamiya Formation at Loc. 5Z261 of the Yurino area. They were identified as *Orthesstheria kokurensis* (the genus *Orthesstheria* has replaced *Euestheria*) by Chen (1996).

According to a recent classification, estherids are formally called Conchostraca, an order of Branchiopoda (Crustacea). Six Recent species are known in Japan, and at least four of them are unique to Japan. All the species of Recent Conchostraca live in very limited environments with very shallow (about 5 to 10 cm, in maximum 20 cm) muddy bottoms which dry up occasionally. Desiccation is indispensable for eggs of Conchostraca to mature. In East Asia, at present, the drying up of lakes takes place in winter. If this was true for Cretaceous time, the Conchostraca could be useful as a indicator of paleoenvironments.

*Sedimentary environments of the ostracode assemblages.*

—The sedimentary environments of the ostracode assemblages described above are discussed below.

#### 1. *Darwinula* assemblage

This assemblage generally suggests such depositional environments as marginal lacustrine bottoms or terrestrial shallow ponds on the fluvial plain. Charophytes, gastropods and plant fragments co-occur abundantly with

ostracodes in poorly sorted sandy siltstone at Loc. TM1. As discussed above, the siltstone containing these kinds of fossils is considered to have been deposited in water shallower than several meters. The bottom was covered with many kinds of aquatic plants, as is easily inferred from numerous plant fossil remains. The water must have been stagnant except for episodic events of storms and floods. Such stagnant and shallow-water environments are supposed to have been in the enclosed part of lacustrine shores shallower than a few meters, or marshes on the fluvial plain.

The assemblage at Loc. 5Z275 must have been in environments somewhat different from those of Loc. TM1, because the sediments at the former locality are made up exclusively of black sandy siltstone with ostracode-crowded layers. The lack of plant fossils suggests that the siltstone was deposited on a bottom deeper than the base of the vertical distribution of aquatic plants (cf. Figure 11), or in open shallow-water environments. The former is considered more probable because of the scarcity of fossils. Moreover, if the latter was the case for Loc. 5Z275, many kinds and large numbers of animals should have lived there. However, the depositional environment is not thought to have been so deep, because it was also inhabited by many individuals of the gastropod *Brotiopsis wakinoensis*. The genus *Brotiopsis* belongs to the Pleuroceridae, almost all the Recent species of which live on lake or river bottoms shallower than several meters.

Far deeper environments are thought to have existed in the surroundings of Loc. 5254 of the Wakino area and Loc. 5251 of the Yurino area, based on analysis of sedimentary facies. Mudstone with thin silty laminae at Loc. 5254 is compared to a deposit resulting from seasonal suspension clouds, and mudstone intercalated by graded sandstone at Loc. 5251 is inferred to be of turbidite origin by Seo *et al.* (1992). These facies are relatively poor in ostracode and other fossils.

In contrast, the depositional environments of the Nyoraida Formation at Loc. 5241 are considered to have been shallow-water ones because of the relative abundance of ostracodes in massive mudstone, presumably bioturbated. This assemblage indicates a subtropical-tropical climate, the work of Ye (1994) having shown that the genus *Darwinula* was widely distributed and able to diversify in southern China, but declined to the north.

#### 2. *Cypridea*? cf. *renalata* subassemblage

This subassemblage is inferred to suggest a fluvial plain, judging from estherid fossils and sedimentary facies. Estherids live only in shallower water than 20 cm, where the bottom is occasionally emerged and dried up. Laterally changeable lithologies from clay to pebbly conglomerate and sedimentary structures such as channel structures and cross-laminations support flood plain environments.

This kind of severe environments for aquatic animals allows ostracode life for only a short term, and so, almost all of the individuals are of small size. The scarcity of ostracodes in the Lower Wakamiya Formation is explained by such a severe environment.

#### 3. *Mongolianella-Cypridea* assemblage

This assemblage at Locs. 5203D and 5203B is presumed to have been on a variable widespread shallow-water bot-



tom, because many kinds of niches seem to have existed in the same water mass, as suggested by the variety of ostracodes and sediments (Matsukawa *et al.*, 1996).

This assemblage at Loc. 5247 shows a lower species diversity ( $\lambda = 0.44$ ) than the ones at Locs. 5203D ( $\lambda = 0.15$ ) and 5203B ( $\lambda = 0.18$ ). It is explained by a relatively deeper environment, which is shown by exclusively abundant charophyte fossils. Such an environment corresponds to the so-called "Chara zone", which is the lowermost zone in the vertical distribution of aquatic plants at water depths from a few to 30 m as already discussed.

#### 4. *Cypridea tera* subassemblage

This subassemblage is known both in the Wakino-Yurino and the southern Kokura area.

With thin parallel laminations of dark gray mudstone intercalated with sandstone, the depositional environment for the *Cypridea tera* subassemblage in the Wakino-Yurino area (Loc. 5467) is inferred to have been similar to that of Locs. 5203D and 5203B: a variable widespread shallow-water bottom. On closer view, the environment at Loc. 5467 seems to have been somewhat antagonistic to ostracodes, as the ostracode-bearing layer is overlain by sandstone as thick as 7 m.

The same subassemblage is in thinly parallel-laminated mudstone intercalated with sandstone at Loc. 5455 in the Gamo block in the southern Kokura area. From the lithological similarity, the depositional environment is inferred to have been similar to that of Locs. 5203D, 5203B and 5467. The environment may have been of widespread shallow-water bottom, though the environment of Loc. 5455 may have been slightly hostile to ostracode life, as sandstone intercalations are relatively frequent.

#### 5. *Eoparacypris* subassemblage

The low diversity of species ( $\lambda = 0.41$ ) in this subassemblage suggests that species of the genus *Eoparacypris* lived in restricted environments. Judging from the lithology without intercalations of sandstone, it is certain that a quiet environment persisted for a long time. According to Anderson (1985), this genus is relatively abundant in marly beds. This may suggest shallow lake environments, where the rate of evaporation was high. However, carbonate is not preserved in any of the studied materials.

#### 6. *Cypridea-Darwinula* assemblage

This assemblage lived in a shallow and enclosed part of the marginal lacustrine environment, because massive sandy mudstone shows repeated bioturbations and sporadically contains granules of secondarily formed iron sulfate. Many kinds of animal fossils other than ostracodes, such as fish, turtles and gastropods occur in this sandy mudstone. The turtle fossils are especially indicative of near-shoreline environments. This sandy mudstone, however, contains few plant fossils, which are generally rich in enclosed parts of the marginal lacustrine environments and terrestrial marshes on the fluvial plain.

According to Ye (1994), the genus *Darwinula* was widely distributed and evolved diversely in southern China while declining to the north in the Late Cretaceous. This means that the genus *Darwinula* preferred a subtropical-tropical climate to temperate-cold one. The occurrence of the genus *Darwinula* indicates that the *Cypridea-Darwinula* assem-

blage existed in subtropical-tropical climates, as did the *Darwinula* assemblage in the Wakino-Yurino area.

#### 7. *Darwinula-Mongolianella-Rhinocypris*?-*Candona* assemblage

This highly diversified assemblage ( $\lambda = 0.11-0.24$ ) at Locs. 5221a, 5221b, 5452 and 5453 was on shallow-water bottoms, which were dried up temporally. Sedimentary structures such as channels and mudcracks and the lithology of reddish sandstone indicate fluvial depositional environments. The topset of deltas may have spread here.

#### 8. Large *Cypridea* subassemblage

This subassemblage must have been under the influence of intense volcanic activity, because the lithology consists mostly of white tuff. Intercalations of poorly sorted reddish sandstone exhibit shallow-water bottoms which saw occasional emergence. It is to be expected that only the extremely large-sized species survived drastic environmental changes caused by ash fall that killed other species which lived there.

#### 9. Nodular *Cypridea* subassemblage

The environment for this subassemblage is inferred to resemble that of the underlying large *Cypridea* subassemblage from the lithology of tuffaceous mudstone at Loc. 5451a. No difference between them has been found.

#### 10. *Mongolianella* Subassemblage

The bottom environment of this subassemblage is similar to that of the large *Cypridea* subassemblage and the nodular *Cypridea* subassemblage, as far as the lithology is concerned.

#### 11. *Rhinocypris* subassemblage

The bottom environment for this subassemblage is presumed to have been almost the same as that for the large *Cypridea* (Loc. 5451a), nodular *Cypridea* (Loc. 5451b), and *Mongolianella* (Loc. 5451d) assemblages in view of the similar lithologies among them.

### Zonation and correlation

Biostratigraphical zonation based on the ostracode assemblages has been established in the Wakino-Yurino area. By using this zonation, the Wakino Subgroup in several blocks of the southern Kokura area is correlated with the formations in the Wakino-Yurino area.

Zonation by ostracode assemblages.—Remarkable shifts in the ostracode assemblages were clearly recognized in the Wakino Subgroup in the Wakino-Yurino area (Figure 9); hence the subgroup can be divided into the following three assemblage zones toward the top of the sequence.

#### 1. *Darwinula* assemblage zone

All the ostracode assemblages from the Sengoku and Nyoraida formations are assigned to the *Darwinula* assemblage (Figure 6). The range of the *Darwinula* assemblage provides a basis for a single biostratigraphical zone. This zone is called here the "*Darwinula* assemblage zone (in brief, a. z.)."

#### 2. Transitional assemblage zone

The *Cypridea*? cf. *renalata* subassemblage was obtained from only one locality, as the Lower Wakamiya Formation is only sparsely fossiliferous (Figure 6). But the subassemblage shows clearly different characteristics from both the



Stratigraphy	Molluscan zone (Ota, 1960)	Molluscan fauna (Hase, 1960)	Fish fauna (Yabumoto, 1994)	Ostracode assemblage zone (this paper)
Upper Wakamiya Fm.	<i>Viviparus onogoensis</i> - <i>Nakamuranaia</i> ? cf. <i>chingshanensis</i> ZONE	Upper Wakino or Wakamiya faunule	<i>Diplomystus</i> - <i>Wakinoichthys</i> fauna	Large Cypridacean Assemblage Zone
Lower Wakamiya Fm.			<i>Paraleptolepis</i> - <i>Wakinoichthys</i> fauna	Transitional Assemblage Zone
Nyoraida Fm.	<i>Brotiopsis wakinoensis</i> ZONE	barren	barren	<i>Darwinula</i> Assemblage Zone
Sengoku Fm.		Lower Wakino or Sengoku faunule	<i>Nipponamia</i> - <i>Aokiichthys</i> fauna	

Figure 12. Comparison among biostratigraphical zonations by various kinds of faunas.

underlying and overlying assemblages. This poorly designated subassemblage is regarded as a "transitional" assemblage from the underlying *Darwinula* assemblage to the overlying cypridacean-dominant assemblages, and defines the "transitional assemblage zone (a. z.)."

### 3. Large Cypridacean assemblage zone

Three different ostracode assemblages were recognized in the Upper Wakamiya Formation, though other formations of the Wakino Subgroup each contain a single assemblage (Figure 6). One of the three assemblages, the *Mongolianella-Cypridea* assemblage, represents a recurrence within the formation. Two of the three assemblages, the *Cypridea tera* subassemblage and the *Eoparacypris* subassemblage are observed at a single locality. The differences among these three subassemblages seem to be determined by environmental differences. Consequently, it is practical to adopt the general characteristics and names of higher taxa. Hence, the Upper Wakamiya Formation is biostratigraphically named the "Large Cypridacean assemblage zone" after large forms of *Cypridea*, *Mongolianella* and *Candona*, all of which belong to the superfamily Cypridacoidea.

This ostracode biostratigraphical zonation is compared with the other biostratigraphical zonations previously proposed on the basis of different kinds of fossils (Figure 12). The Nyoraida Formation, which has been biostratigraphically considered to be barren by Hase (1960) and Yabumoto (1994) and assigned to the lower part of the molluscan *Viviparus onogoensis*-*Nakamuranaia*? cf. *chingshanensis* zone by Ota (1960) (originally, he described it as the *Viviparus onogoensis*-*Nakamuranaia*? sp. cf. *N. chingshanensis* zone), was assigned to the upper part of the *Darwinula* assemblage zone in the ostracode zonation. The Lower Wakamiya and Upper Wakamiya Formations can be distinguished from each other by the ostracode zonation in the same ways as the fish zonation by Yabumoto (1994), though they cannot be discriminated by the molluscan zonation (Ota, 1960; Hase, 1960).

Correlation of formations in the southern Kokura area.—In the southern Kokura area, the Wakino Subgroup is divided into many blocks by faults. Owing to such complicated geological structures, it is difficult to determine the exact stratigraphical positions of the exposure at each block.

Therefore, the same block has been regarded as different formations by previous studies.

#### 1. Dobaru block

The strata which have been assigned to the W1 formation (Ota, 1955, 1960; Hase, 1958) and contain the *Cypridea-Darwinula* assemblage in the Dobaru block were correlated with the Sengoku or Nyoraida Formation of the Wakino-Yurino area by ostracode biostratigraphy, because the *Cypridea-Darwinula* assemblage from the lower stratigraphical part in the Dobaru block is similar to the *Darwinula* assemblage from the Sengoku and Nyoraida Formations in the Wakino-Yurino area in the abundance of *Darwinula*. However, there is a great difference in the abundance of the genus *Cypridea*. This is probably owing to the rareness of plants covering the bottom, as described above in this section. No species of *Cypridea* in the *Cypridea-Darwinula* assemblage is in common with those of the five assemblages and subassemblages in the Lower Wakamiya and Upper Wakamiya Formations of the Wakino-Yurino area. This fact also supports the above correlation. During the early depositional stage of the Wakino Subgroup, in which *Darwinula* was dominant, the deeper and stagnant nearshore water environments probably allowed ancestral species of *Cypridea* to live. *Damonella* cf. *ovata*, known only from the *Darwinula* a. z. and occurring in both the *Cypridea-Darwinula* assemblage and the *Darwinula* assemblage, also strengthens the correlation.

#### 2. Gamo blocks

The sediments in the Gamo block were correlated with the Upper Wakamiya Formation in the Wakino-Yurino area, because they contain the same *Cypridea tera* subassemblage belonging to the Large Cypridacean assemblage zone in the Wakino-Yurino area.

The block has been assigned to the W4 formation in the previous studies (Ota, 1957, 1960; Hase, 1958; Ota *et al.*, 1979). The ostracode zonation leads to the same conclusion.

#### 3. East Kumagai and Washimine blocks

The East Kumagai block has been regarded as distributing the W3 formation by Ota (1957, 1960) and Hase (1958). Recently, however, Sakai *et al.* (1992) considered it to be "Unit B" of their subdivisions of the Wakino Subgroup in Yamada Park of Kokura. On the other hand, the strata in



the Washimine block have been assigned to different formations by different authors; for example, to the W3 formation by Ota (1957, 1960), equivalent of the Nyoraida (W2) Formation by Hase (1958), and "Unit A" by Sakai *et al.* (1992).

Both the Lower Cretaceous strata in the East Kumagai and Washimine blocks yield the same high-diversity (5453:  $\lambda = 0.12$ , 5221a, 5221b:  $\lambda = 0.11$ , 0.12) ostracode assemblage. The *Darwinula-Mongolianella-Rhinocypris*?-*Candona* a. z. shows some relations to the *Mongolianella-Cypridea* assemblage that belongs to the large Cypridacean a. z. in the Wakino-Yurino area, because it contains *Cypridea kyushuensis*, which is one of the characteristic species of the *Mongolianella-Cypridea* assemblage. Such relations are also shown by the abundance of *Mongolianella*.

On the other hand, the abundance of *Darwinula* suggests subtropical-tropical climates. *Lycopteroocypris* cf. *sinuolata* from the East Kumagai block is common with the *Cypridea-Darwinula* assemblage of W1 formation in the Dobaru block.

*Rhinocypris* cf. *jurassica* from the East Kumagai block is found only in the transitional a. z. in the Wakino-Yurino area. In the southern Kokura area, however, this species survived until the depositional time of the West Kumagai block, which may be assigned to the large Cypridacean a. z. as discussed below.

In summary, the strata bearing the *Darwinula-Mongolianella-Rhinocypris*?-*Candona* a. z. in the East Kumagai and Washimine blocks are correlated with the transitional a. z. in the Wakino-Yurino area, namely, with the Lower Wakamiya Formation.

#### 4. West Kumagai block

The West Kumagai block has been considered to be occupied by the W3 formation (equivalent to the Lower Wakamiya Formation) by Ota (1957, 1960) and Hase (1958), though Ota *et al.* (1979) regarded the strata in the block as the W4 formation (the Fourth Formation). Recently, Sakai *et al.* (1992) assigned it to "Unit B", which overlies "Unit A".

The block contains four ostracode subassemblages: the large *Cypridea*, nodular *Cypridea*, *Mongolianella* and *Rhinocypris* ones in ascending order. These four assemblages have common characteristics with one another; all of them contain large-sized species or nodulate species of the superfamily Cypridoidea. They are *Cypridea* sp. 5, *Mongolianella* cf. *palmosa*, *M. zerussata longiuscula*, "*Cypridea* (C.) sp. 4" of Paik *et al.* (1988), *Rhinocypris* cf. *tuberculata* and "*Rhinocypris* sp. 1" and "*R. sp. 2*" of Cao (1996). These characteristics lend themselves to the correlation with the large Cypridacean assemblage zone in the Wakino-Yurino area. Therefore, the strata in the West Kumagai block were correlated with the Upper Wakamiya Formation.

#### 5. Stratigraphy and geological structure of the Wakino Subgroup

In conclusion, the ostracode biostratigraphy revealed that the stratigraphy and geological structures in the southern Kokura area are as follows.

The formations previously called the W1, W2, W3 and W4 formations are formally called here the Sengoku, Nyoraida, Lower Wakamiya and Upper Wakamiya Formations, respectively, because the ostracode biostratigraphical zonation that

has been established in the type areas is well discernible in the southern Kokura area.

The Sengoku Formation in this area consists of more fine-grained sediments, and secondarily formed iron in them shows a more reducing environment than in the Wakino area. The Lower Wakamiya Formation in this area was deposited in widespread shallow water and rarely dried-up environments, because it yields much abundant in the way of ostracode fossils than in the Yurino area. In contrast to the Sengoku and Lower Wakamiya Formations, the Nyoraida and Upper Wakamiya Formations in this area do not seem to be different from the Wakino-Yurino area.

In the Dobaru district, the Wakino Subgroup begins with the Sengoku Formation, which clino-unconformably overlies the Paleozoic strata. The Sengoku and the overlying Nyoraida Formations are distributed with a northward dipping structure, and are faulted to bound on the basement rocks or intrusive rocks.

In the northern part of the area, the Lower Wakamiya and Upper Wakamiya Formations are distributed in a principal anticline. Specifically, the Upper Wakamiya Formation is distributed in the southern Gamo block and the northern West Kumagai block, and the Lower Wakamiya Formation is in the Washimine and East Kumagai blocks, both of which are situated in an axial part of the anticline. In detail, however, many small faults and foldings are involved in places in this area.

## Conclusions

As the first biostratigraphical study on Mesozoic nonmarine ostracodes in Japan, 11 assemblages have been established, and the zonation based on these assemblages has been proposed. Major results of these investigations are summarized as follows:

1) From the Wakino Subgroup in the Wakino-Yurino area, five assemblages and subassemblages were recognized: the *Darwinula* assemblage from the Sengoku and Nyoraida Formations, the *Cypridea*? cf. *renalata* subassemblage from the Lower Wakamiya Formation, and the *Mongolianella-Cypridea* assemblage, the *Cypridea tera* subassemblage and the *Eoparacypris* subassemblage from the Upper Wakamiya Formation.

2) Based on stratigraphical changes in general features of these assemblages, stratigraphical zonation by ostracodes was proposed as the *Darwinula* a. z. (assemblage zone), transitional a. z. and large Cypridacean a. z. in ascending order. This method of zonation is reasoned by vertical changes of the ostracode assemblages. These assemblages were easily recognized because of their characteristic species composition. This probably is due to the absence of water birds as main transporters of ostracode eggs, though ostracode eggs of shoreline-inhabiting species could have been transported by shore birds.

3) In the southern Kokura area, seven ostracode assemblages and subassemblages were recognized in the Wakino Subgroup in five blocks: the *Cypridea-Darwinula* assemblage from the W1 formation in the Dobaru block, the *Cypridea tera* s. a. in the Gamo block that has been assigned to the W4 formation, the *Darwinula-Mongolianella*



*Rhinocypris*?-*Candona* assemblage in the Washimine and East Kumagai blocks, the large *Cypridea*, nodular *Cypridea*, *Mongolianella* and *Rhinocypris* subassemblages from the West Kumagai block. With regard to the stratigraphical zonation proposed in the Wakino-Yurino area, each of the blocks was correlated as follows: the strata in the Gamo block certainly belong to the large Cypridacean a. z., those in the Washimine and East Kumagai blocks are probably assigned to the transitional a. z., and the West Kumagai block is surely attributed to the large Cypridacean a. z.

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# Further notes on the turrilitid ammonoids from Hokkaido— Part 2 (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin—XC)

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**Abstract.** Six species of *Turrilites*, two species of *Mesoturrilites* and two species of *Mariella* are described on the basis of material from the lower and middle parts of the Cenomanian (mid-Cretaceous) in the central and northwestern Hokkaido. Several of them are well known for their worldwide distribution and occur in Hokkaido at correlatable stratigraphic levels. Three new species, *Turrilites complexus*, *T. miroku* and *Mesoturrilites pombetsensis*, are established, showing interesting but still questionable relationships with some previously known ones. Two species in open nomenclature require further study.

**Key words:** Cenomanian, Hokkaido, *Mariella*, *Mesoturrilites*, *Turrilites*

## Introduction

The material from the Cretaceous Yezo Group of Hokkaido provides not only examples of well known, widespread species but also of other, little known or new ones. Selected examples of both categories are studied to improve systematic, biostratigraphic and biogeographic knowledge. The studied specimens came primarily from the Cenomanian of the Ikushunbetsu Valley of the Mikasa district, central Hokkaido, and the Abeshinai-Saku area of the Nakagawa district, northwestern Hokkaido. For the stratigraphy of the two areas, readers may refer to the two papers: Matsumoto (compiled, 1991, p. 3–5, 21–24) for the former and Matsumoto (1942, p. 180–214) for the latter. The material depends primarily on the collections of T. T. and T. M. In addition to them several specimens from these and also adjacent areas treated in the two papers written in Japanese, i. e., Nishida *et al.* (1997) and Hayakawa and Nishino (1999) are cited with brief remarks. An additional specimen from Abeshinai has been provided by M. Okamura.

**Repositories.**—The specimens treated in this paper are officially registered in the following institutions, with prefixes:

GK: Geological Collections, Kyushu University Museum, Fukuoka, 812-8581, Japan

GS: Geological Collections in Saga University, Saga, 840-8502, Japan

IGPS: Museum of Natural History, Tohoku University, Sendai, 980-8578, Japan

NMA: Nakagawa Museum of Natural History, Nakagawa, 098-2802, Hokkaido, Japan

UMUT: University Museum, University of Tokyo, Hongo, Tokyo, 113-0033, Japan

The specimen collected by T. T. is indicated with the previous number in brackets. Likewise, the specimen collected by T. M. and once stored in Umut under the heading of GT is indicated in brackets, for it is now officially transferred to GK.

## Systematic descriptions

(continued from Part 1)

Genus *Turrilites* Lamarck, 1801

**Type species.**—*Turrilites costatus* Lamarck, 1801 (p. 101) by original designation.

**Diagnosis.**—Tightly coiled turrilitids with small apical angle. Ribs with no or two to four rows of tubercles; ribs and tubercles equal in number in all rows (modified from Wright and Kennedy, 1996, p. 349).

**Remarks.**—Besides well known *T. scheuchzerianus* Bosc, 1801, *T. costatus* Lamarck, 1801 and *T. acutus* Passy, 1832, two new species established below occur in the Cenomanian of Hokkaido.

*Turrilites complexus* sp. nov.

Figures 1, 2, 3A–D



**Figure 1.** *Turrilites complexus* sp. nov. **A, B.** GK.H8552 (holotype). **C, D.** GK.H8553. **E.** GK.H8554. **A, C, E:** lateral views. **B, D:** basal views. Figures are all  $\times 1.5$ . Photos courtesy of M. Noda.



**Table 1.** Measurements of *Turrilites complexus* sp. nov.

Specimen	NW	Hp	Ht	D	ap	h	d	h/d	R(T)
GK.H8552	9.0	84.0	102.0	30.0	20°	12.0	23.5	0.51	26-22
GK.H8553	8.5	87.0	105.3	33.5	19°	14.5	28.2	0.51	22-16
GK.H8554	7.0	103.5	133.0	31.0	20°	15.5	31.0	0.50	24-17
GK.H8550	7.5	40.7	55.0	16.8	22°	7.2	15.0	0.48	31-22
NMA-151	7.5	33.8	—	13.6	19°	5.3	11.0	0.48	27-23 (?)

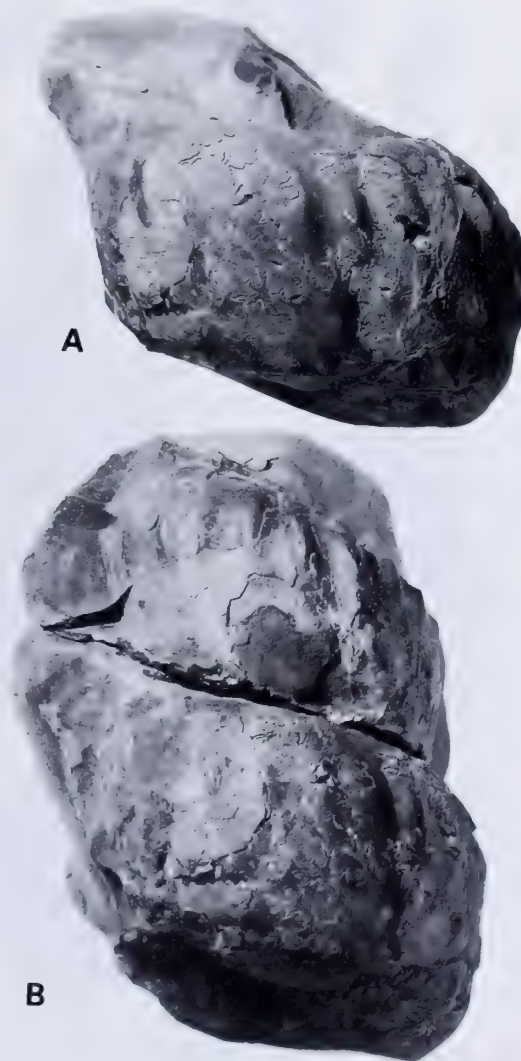
NW = number of preserved whorls, Hp = total height of the preserved shell, Ht = total height of shell from the preserved last whorl to the estimated apex, D = diameter of the preserved last whorl, ap = estimated apical angle. h = height of an exposed flank of a late whorl, diameter of the same whorl, R or T = number of ribs or tubercles in a given row per whorl, showing change with growth, if any. Linear dimension is in mm.

**Material and occurrence.**—Holotype is GK.H8552 [= previous S.40-5-16] (Figure 1A, B; Figure 3A, B) collected by T. T. in 1965 at Loc. Ik1100, on the right side of the River Ikushunbetsu, from the lower part of the Member IIb of the Mikasa Formation (see Matsumoto, 1991, p. 22, fig. 1). Paratypes from the type locality are GK.H8550 [= S.39-4-27] (Figure 3C, D), GK.H8553 [= S.40-8-7] (Figure 1C, D) and GK.H8554 [= S.50-4-13] (Figure 1E), collected by T. T. in 1964, 1965 and 1975 respectively. Another paratype is a large but incomplete specimen, GK.H8558 [= previous GT. I-3150] (Figure 2A, B), collected by T. M. in 1938 at Loc. T591b on the left side of the River Abeshinai of the Nakagawa district. Also NMA-151, collected by T. Nishino at "Loc. Y" [Yasukawa] and illustrated by Hayakawa and Nishino (1999, pl. 10, fig. f) as *T. costatus*, should now be transferred to this species. There are more examples from both Mikasa and Nakagawa districts, but at present they belong to private possessions.

**Diagnosis.**—Turreted shell with a low apical angle, showing the ontogenetic change of ornamentation from numerous, crowded ribs with scarcely discernible tubercles to the diagnostic ribs with tubercles of moderate intensity like *Turrilites costatus*. In addition to the three rows of ribs or tubercles like those of *T. costatus*, there are clavate small tubercles of the fourth row, from which radial ribs run on the lower (or basal) surface to the narrow umbilicus. The concave zone between the upper and lower ribs is faint in youth, moderately distinct in the middle or main stages, and may become indistinct at the last stage.

**Description.**—The available specimens are scarcely affected by secondary deformation. They are, however, incomplete in that the very apex is lacking and their last whorl is more or less deficient. The holotype (Figure 1A, B; Figure 3A, B) and a paratype, GK.H8553 (Figure 1C, D) are slightly over 100 mm in the original height. In both specimens the preserved last whorl is still septate. GK.H8554 (Figure 1E) is the largest of the four specimens from the type locality, showing 133 mm in the total height of the shell. The body chamber is preserved in this specimen, but its apertural part is destroyed. GK.H8550 (Figure 3C, D) shows the characters of the young shell, although the initial part is lacking.

Despite some deficiencies mentioned above, they show as a whole the above-described diagnostic characters. This is also supplemented by the measurements (Table 1).



**Figure 2.** *Turrilites complexus* sp. nov. **A, B.** GK.H8558. **A** is the detached lower whorl of **B** and slightly turned clockwise to show clearly the saddle between E and L. Figures are  $\times 1$ . Photos by C. Ueki.



Minor differences between specimens can be regarded as infraspecific variation. For instance, the decrease in the rib density with growth varies from individual to individual (see Figure 4). The tubercles on the last whorl of GK.H8554 (Figure 1E) become weaker than those of the preceding whorls, but a similar feature often occurs in the last whorl of the turrilitid ammonoids.

The septal suture at a young stage is exposed partly on GK.H8550. L is situated on the concave zone between the

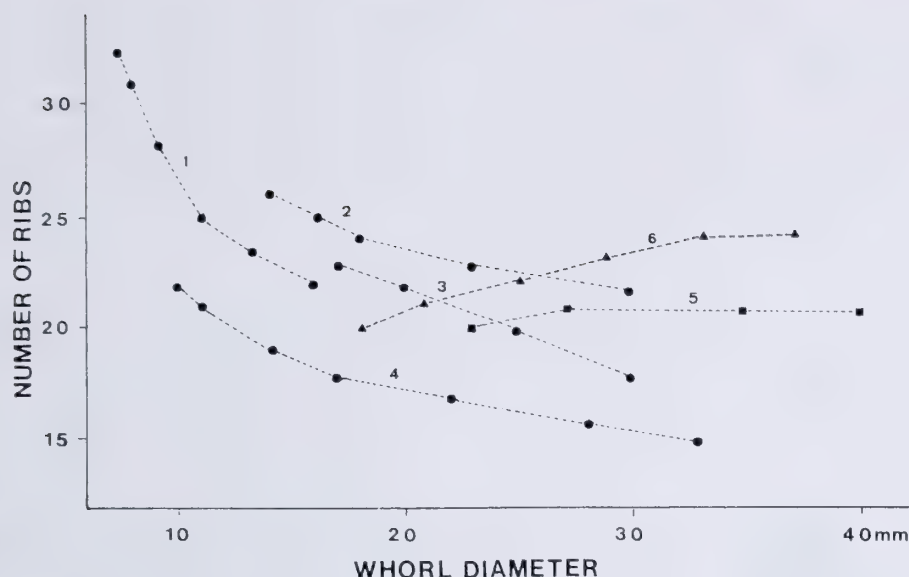
upper and lower ribs. The suture of a late growth stage is much incised (see Figure 2). The E-L saddle is so broad that L is shifted toward the lower whorl seam and U is in the middle part of the lower whorl face (Figure 2A). The incised branches of an element (probably I) are extended from the concealed side (Figure 2B).

*Comparison and discussion.*—With respect to the characters of the middle to late growth stages this species resembles *Turrilites costatus* Lamarck, but it is distinguished by the



**Figure 3.** A-D. *Turrilites complexus* sp. nov. A, B. GK.H8552 (holotype). Fig. 3A is 180° turned from Fig. 1A; Fig. 3B is another basal view in a different light from Fig. 1B. Figures slightly over natural size. C, D. GK.H8550, lateral and basal views,  $\times 2$ . E, F. *Turrilites* aff. *costatus* Lamarck. GK.H8549, lateral and basal views,  $\times 2$ . G. *Turrilites scheuchzerianus* Bosc, 1801. GK.H8563, half exposed from the rock matrix,  $\times 1.5$ . H, I. *Turrilites costatus* Lamarck, 1801. H. GK.H1373,  $\times 2$ . I. GK.H8560,  $\times 1$ . J-M. *Turrilites acutus* Passy, 1832. J. GS.G114,  $\times 2$ . K. GS.G113,  $\times 2$ . L. GS.G127,  $\times 1.7$ . M. GK.H8559,  $\times 1$ . N. *Mesoturrilites* cf. *aumalensis* (Coquand). GK.H8562,  $\times 2$ . Photos courtesy of M. Noda (A-D), N. Egashira (G, H, J-L) and C. Ueki (I, M, N).





**Figure 4.** Diagram showing the ontogenetic change of rib density in some representative specimens of *Turrilites complexus* sp. nov. (small solid circle), *Turrilites costatus* Lamarck (solid square), and *Turrilites scheuchzerianus* Bosc (solid triangle). 1: GK.H8550, 2: GK.H8552 (holotype), 3: GK.H8554, 4: GK.H8553, 5: GK.H8560, 6: BG5 GSM 7772 (Sharpe, 1857, pl. 26, fig. 1).

presence of spirally elongated tubercles of the fourth row. In younger growth stages the two species are undoubtedly different in ornamentation. Also, as is shown in Figure 4, in contrast to the ontogenetic decrease of rib density in *T. complexus*, *T. costatus* maintains uniform density with growth.

With respect to the morphological characters of young shells this species resembles *Turrilites scheuchzerianus* Bosc in showing interrupted ribs on rather flat or only gently convex flank, without or with very faintly appeared swellings. The number of ribs seem to vary between individuals in *T. scheuchzerianus*, but the decrease of the number with growth is not so remarkable as in *T. complexus*. Again, the presence of the clavate tubercles of the fourth row in *T. complexus* is a distinction. As to the characters of the middle to late stages *T. complexus* is clearly different from *T. scheuchzerianus*.

Stratigraphically *T. complexus* first appears from a lower level than *T. scheuchzerianus* and *T. costatus*. Hence, it can be presumed that the latter two species may have branched from the former almost simultaneously or successively at slightly different times.

The middle-aged shell of this species resembles *Mariella* (*Mariella*) *oehlerti* (Pervinquière, 1910) (see also Matsumoto *et al.*, 1999, p. 109, figs. 2-4; Matsumoto *et al.*, 2000, p. 8, fig. 3) in the whorl shape and ornamentation. The latter shows a wide extent of variation in the density of tubercles, as Klinger and Kennedy (1978, p. 32, fig. 9) have demonstrated. But the ontogenetic change of ornament in the latter species is not so great as in *T. complexus*. On the average tubercles are predominant over ribs in *M. (M.) oehlerti*, but ribs in the upper row characterize the middle-aged whorls of *T. complexus* as in the main part of the *T. costatus* shell. The spirally elongated tubercles of the

fourth row are common in *M. oehlerti* and *T. complexus*.

There is, however, to some extent infraspecific variation. For instance, Klinger and Kennedy (1978, p. 33) pointed out the presence of "variety A" in *M. (M.) oehlerti* "which differs from the "typical form" in possessing moderately to well-developed ribs". Numerous specimens of *M. (M.) oehlerti* from Zululand and Natal in South Africa seem to be more or less fragmentary, as are shown by the illustrations by Klinger and Kennedy (1978, pl. 6, figs. H-N, P; pl. 7, fig. G). If fragmentary pieces of a middle-aged shell of *T. complexus* were mixed with them, they might be regarded as the ribbed variety of *M. (M.) oehlerti*.

**Discussion.**—This species occurs in the lower part of the Member IIb of the Mikasa Formation. This unit is biostratigraphically defined as the Zone of *Mantelliceras japonicum* - *Sharpeiceras kongo*, that is, the second unit in the three subdivisions of the lower Cenomanian in the Ikushunbetsu Valley. It was erroneously listed as *Turrilites costatus* in the stratigraphic notes by Matsumoto *et al.* (1969, p. 287) and also Matsumoto (*in*, Matsumoto, 1991, p. 22). It occurs also in the Abeshinai Valley of the Nakagawa district. A specimen from Loc. T591b is referable to the middle or upper part of the lower Cenomanian, because Loc. T591b is above Loc. T591a, where *Mesoturrilites* cf. *aumalensis* (Coquand, 1862) (see description in later pages) was obtained, and well below Loc. T591d, where *Turrilites acutus* Passy, 1832 (see below) occurred. The "Locality Y" of Yasukawa, where a specimen of *T. complexus* (NMA-151) was collected, is a fairly extensive exposure of strata, about 70 m in thickness, but the stratigraphic level of NMA-151 is not precisely recorded by Hayakawa and Nishino (1999). Although they ascribed the entire thickness of the exposed strata of "Loc. Y" to the middle Cenomanian, the assignment is questionable, because *Cunningtoniceras*

**Table 2.** Measurements of *Turrilites costatus* Lamarck.

Specimen	NW	Hp	Ht	D	ap	h	d	h/d	R(T)
GK.H8560	6	105.0	150.0	41.0	20°	20.0	37.0	0.54	22
NMA-145	5	115.0	165.0	45.0	23°	24.0	42.5	0.56	ca.21

Legend as for Table 1. In NMA-145 about 120° of each whorl is embedded in the rock matrix.

**Table 3.** Measurements of *Turrilites* aff. *costatus* Lamarck.

Specimen	NW	Hp	Ht	D	ap	h	d	h/d	R(T)
GK.H8549	8.0	19.6	20.8	10.2	3°	3.7	8.0	0.46	15-24

Legend as for Table 1.

sp., an index of middle Cenomanian, was obtained, according to the collector (Yutaka Koike), from the uppermost part of the sequence.

At present this species is known to occur only in Japan. In view of the worldwide distribution of *T. scheuchzerianus* and *T. costatus*, whether *T. complexus* has a more extensive distribution should be clarified.

#### *Turrilites scheuchzerianus* Bosc, 1801

Figure 3G

*Turrilites scheuchzerianus* Bosc, 1801, p. 190; Wright and Kennedy, 1996, p. 349 (with full synonymy)

**Type.**—"The status and whereabouts of the type material (Bosc, 1801, p. 190) have not been well established" (Wright and Kennedy, 1996, p. 349).

**Material.**—GK.H8563 [= previous GT.I-3154] (Figure 3G) collected by T. M. from a floated nodule at Loc. T32-33p, Saku-gakko-no-sawa, Nakagawa district. NMA-144, NMA-143 and NMA-142, collected by T. Nishino from "Loc. T" of Nakagawa district and described in Japanese by Hayakawa and Nishino (1999, p. 11, pl. 10, figs. a, b-c, e).

**Descriptive remarks.**—This species has been amply described and discussed by Wright and Kennedy (1996, p. 349, pl. 106, figs. 7, 8, 11, 12; pl. 107, figs. 1-7; text-figs. 137G, J; 138C, D, F-I, N; 139D-I; 140A, D-I; 143H; 147A, B) on the basis of numerous specimens from South England and extensive regions in the world. In addition to the specimens reported by Hayakawa and Nishino (*vide supra*), we know that a well preserved specimen occurred in the Zone of *Cunningtoniceras takahashii* at Loc. Ik1051b of the Ikushunbetsu Valley. It is quite similar to a British specimen (BMNH 30210, Wright and Kennedy, 1996, pl. 107, fig. 7), but it is not officially registered.

**Distribution.**—Middle part of the Cenomanian in Hokkaido. For the range in South England and the worldwide distribution see Wright and Kennedy, 1996, p. 353.

#### *Turrilites costatus* Lamarck, 1801

Figure 3 H, I

*Turrilites costatus* Lamarck, 1801, p. 102 (pars); Wright and Kennedy 1996, p. 354, pl. 103, figs. 1, 2, 5; pl. 104, figs. 1-4, 6, 8-10; pl. 105, figs. 1, 5, 6, 10, 12, 13, 16, 17, 19; pl. 106, figs.

1-6, 9, 10; text-figs. 137C; 139A-C; 142A, F, G; 143A-G, L-P (with full synonymy).

**Type.**—The specimen from Rouen figured by Douvillé (1904, p. 54a, fig. 1) in the Lamarck Collection is the lectotype designated by Kennedy (1971, p. 30). It is kept in the Muséum National d'Histoire Naturelle, Paris and was reillustrated by Wright and Kennedy (1996, text-fig. 142F).

**Material and occurrence.**—GK.H8560 [= GT.I-3157a] (Figure 3I) and GK.H8561 (not figured) collected by T. M. in 1938 on the left side of the River Shakotan [= Sakugawa]; NMA-176 and NMA-145 collected by T. Nishino from "Loc. T" on the right bank of the River Teshio, all in the Nakagawa district. GK.H1373 (Figure 3H) collected by T. M. in 1939 from Loc. Y524, Tengu-zawa of the Shuparo area (for the location see Matsumoto, 1942, pl. 25).

**Descriptive remarks.**—This specimen is well defined by previous authors, especially by Wright and Kennedy, 1996 (*vide supra*). GK.H8560 is a good example from Hokkaido, for it resembles the lectotype. NMA-145 could be regarded as a passage form to *T. acutus* Passy in its pointed tubercles. It is, however, quite similar to GK.H8560 (see ap, h/d and R(T) in Table 2).

**Distribution.**—The described specimens from Hokkaido are of middle Cenomanian age. For the range in England and also worldwide distribution of this species see Wright and Kennedy, 1996, p. 358.

#### *Turrilites* aff. *costatus* Lamarck, 1801

Figure 3 E, F

**Material.**—A single specimen, GK.H8549 [= previous S.4 3-5-7] (Figure 3E, F) collected by T. T. in 1968 at Loc. Ik1100 from the lower part of the Member IIb of the Mikasa Formation.

**Descriptive remarks.**—This is a small, probably immature specimen. It looks like *T. costatus*, but it shows a larger apical angle and lower whorls in comparison with the latter (compare Table 3 with Table 2). Its younger whorls show rather prominent tubercles in the upper row at moderate intervals (15-17 per whorl) and corresponding number of small tubercles in the lower row. Hence, the young shell is rather similar to *T. acutus* (*vide post*). The later whorls have tuberculated ribs like those of *T. costatus*, but they are rather



**Table 4.** Measurements of *Turrilites acutus* Passy.

Specimen	NW	Hp	Ht	D	ap	h	d	h/d	T
GK.H8559	3	40.0	77.0	32.5	27°	12.0	25.0	0.48	20
NMA-131	6	50.0	60.0	25.0	30°	9.0	19.0	0.47	18
GK.H8551	9	175.0	—	ca.77	—	ca.32	ca.67	ca.0.48	20

Legend as for Table 1. GK.H8551 is so much deformed that D and d are roughly estimated on the basis of the measured maximum and minimum dimensions.

crowded and numerous (24 in the preserved last whorl). There are closely set two rows of spirally elongated tubercles along the lower whorl seam. Thus, the shell of this stage is similar to the middle-aged shell of *T. complexus*. The morphological characters of the still later stage of this specimen are not known.

Despite the incomplete preservation, the specimen is so peculiar that it is tentatively described under the above heading. Its relation with *Mariella* (*M.*) *oehlerti* (Pervinçière, 1910) (see Matsumoto *et al.*, 1999) should be examined on the basis of further material.

#### *Turrilites acutus* Passy, 1832

Figures 3 J-M, 5, 6

*Turrilites acutus* Passy, 1832, p. 9, pl. 16, figs. 3, 4; Wright and Kennedy, 1996, p. 358, pl. 103, fig. 3; pl. 104, figs. 5, 7, 11; pl. 105, fig. 21; pl. 108; figs. 1-4, 8, 11, 12; text-figs. 138M; 141A; 146N-O (with full synonymy).

**Lectotype.**—The original of Passy, 1832, pl. 16, fig. 3 by the subsequent designation of Juignet and Kennedy, 1977, p. 65. For its photographic illustration see Wright and Kennedy, 1996, pl. 108, fig. 8a-c.

**Material and occurrence.**—GK.H8559 [= previous GT.I-3155] (Figure 3M) collected by T. M. in 1938 at Loc. T591d, a cliff on the left side of the River Abeshinai and NMA-131 collected by Nishino from "Loc. T" on the right bank of the River Teshio (Hayakawa and Nishio, 1999, p. 11, pl. 10, fig. h), both in the Nakagawa district. GS.G113, GS.G114 and GS.G127 (Figure 3K, J, L; reproduced here from Nishida *et al.*, 1997, pl. 7, figs. 10, 11 and pl. 12, fig. 5) collected by Kawashita and Egashira from a floated nodule in the Fuku-no-sawa, a branch of the River Shumarinai in the Soeushinai area (for the location see Nishida *et al.*, 1997, text-fig. 8). GK.H8551 [= previous S.43-4-30] (Figure 5) collected by T. T. in 1968 at Loc. Ik1102, north side of the River Ikushunbetsu, from the bed with *Cunningtoniceras takahashii* (Matsumoto). The above records of occurrence all indicate a middle Cenomanian age.

**Diagnosis.**—On the basis of the previous works the diagnosis may be written as follows. A species of *Turrilites* characterized by pointed tubercles of two rows on the flank, with a concave zone between them, and also clavate smaller tubercles of the third row along the lower whorl seam; the upper tubercles are bullate upward; weak radial ribs may run on the lower surface at least partly. Whorls are rather low, showing h/d below 0.5; hence the apical angle is normally 25°–30°.

**Description.**—GK.H8559 is similar to the lectotype and some other specimens of the corresponding growth stage, e. g., those illustrated by Wright and Kennedy (1996, pl. 106, figs. 1, 2, 8, 17) or by Atabekian (1985, pl. 29, figs. 1, 2, 4).



**Figure 5.** *Turrilites acutus* Passy, 1832. GK.H8551. Lateral view of a deformed specimen,  $\times 0.8$ . Photo courtesy of M. Noda.

On the basal surface of GK.H8559 weak radial ribs run from the clavate tubercles of the third row, showing a gentle curvature. The suture is well shown on this specimen (Figure 6). It is essentially similar to the suture illustrated by Atabekian (1985, pl. 29, figs. 1a, 1b).

GK.H8551 is a large specimen, although it is deformed. The diagnostic characters are clearly manifested by its main part, but in its later whorls the tubercles are rather blunt and transitional to longer ribs (see Figure 5).

*Distribution.*—Middle Cenomanian in Hokkaido. For the worldwide distribution see Wright and Kennedy (1996, p. 361).

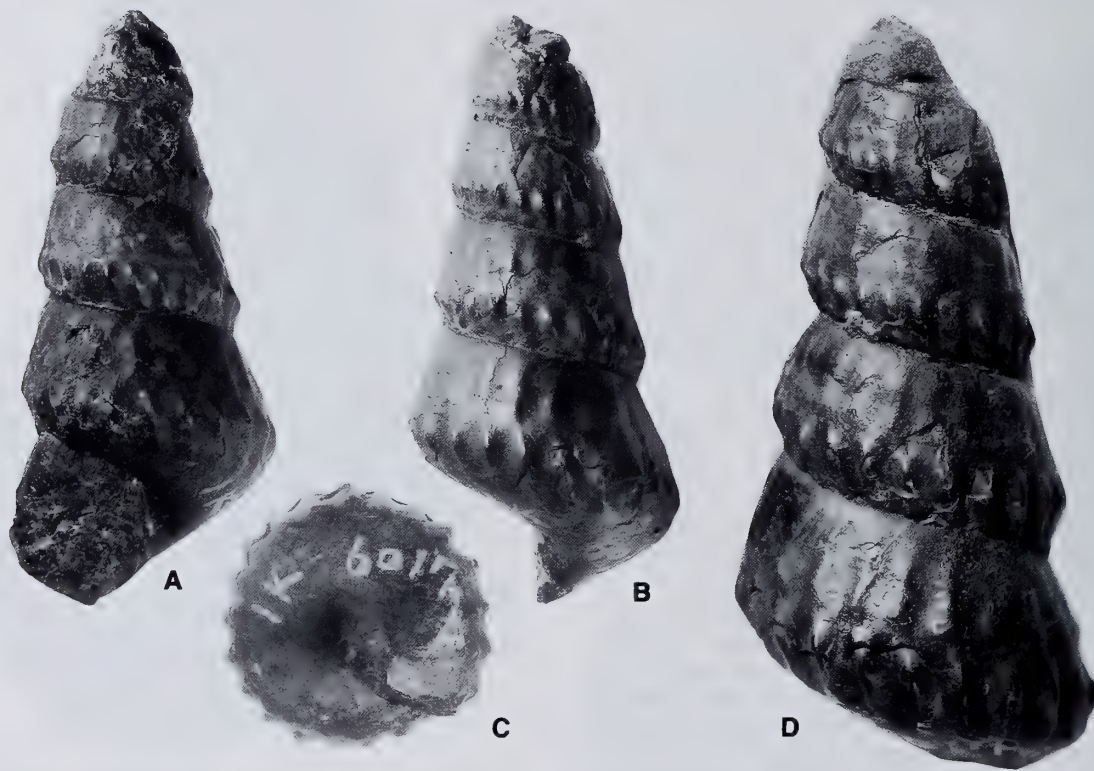
***Turrilites miroku* sp. nov.**

Figure 7

*Material.*—Holotype, here designated, is GK.H5916 from Loc. Ik1067p, Shimo-ichino-sawa of the Ikushunbetsu



**Figure 6.** *Turrilites acutus* Passy, 1832. Septal suture of GK.H8559 at  $h = 12.5$  mm. Broken line = whorl seam, dotted line = approximate outline of a tubercle or rib, E = external lobe, L = lateral lobe, U = umbilical lobe. A branch of an internal element (probably I) is extended from the unexposed side. Figure is about  $\times 4$ . Drawing by T. M.



**Figure 7.** *Turrilites miroku* sp. nov. GK.H5916 (holotype). Two lateral (A and B turned  $180^\circ$ ) and basal (C) views; also another lateral view (D) which is turned  $120^\circ$  anticlockwise from A. A–C are  $\times 1$ ; D is  $\times 1.5$ . Photos courtesy of M. Noda.



**Table 5.** Measurements of *Turrilites miroku* sp. nov.

Specimen	NW	Hp	Ht	D	ap	h	d	h/d	R(T)
GH.H5716	4	68.0	107.0	31.0	21°	13.0	23.0	0.57	22

Legend as for Table 1.

Valley.

**Specific name.**—Miroku [= Maitraya in Sanskrit], a deity in Buddhism, who will help people in the remote future.

**Diagnosis.**—A species of *Turrilites* with small apical angle. Each whorl is characterized by downward steeply inclined flat flank, with its maximum diameter at the level of lower tubercles. The upper, longer ribs rather weak and faintly tuberculated at their lower end. Lower ribs short, prorsiradiate, and sharply tuberculated in their upper part, terminating at the smaller tubercles of the third row aligned along the lower whorl seam. The lower (or basal) whorl face gently convex and nearly smooth.

**Description.**—The holotype consists of four whorls of 68 mm in total height. It lacks the whorls of the early and also the last stages. Assuming that one more whorl is the lost body chamber, the restored shell would be at least 105 mm in total height and 40 mm in diameter of the basal surface. The estimated apical angle is 21°.

Each whorl of this specimen shows a peculiar shape, for its main part of the flank is flat, without convexity, and steeply inclines downward to the level of the prominent tubercles in the lower part, where the maximum diameter is located. Downward from this level, the lower portion of the flank inclines inward for a short distance to the lower whorl seam. Whorls are tightly in contact. The ratio of height (h) to diameter (d) in each whorl, excluding the unexposed lower surface, distinctly exceeds 0.5 (see Table 5).

The ornament is also peculiar to this species. The ribs on the upper flank are weak but moderately numerous, 22 per whorl. Each of them terminates at a small and blunt tubercle. Below this first row of tubercles there is a narrow and shallow, spiral groove; then comes the second row of moderately prominent tubercles, where the flank is somewhat angular at the tubercle or shouldered along the interspace. A short but sharp rib runs from each tubercle of the second row downward to a less prominent small tubercle of the third row, which runs along the lower whorl seam. The upper ribs run transversally with slight curvature, whereas the lower ribs are clearly prorsiradiate together with the bullate tubercles. Lower or basal surface of the whorl is almost smooth and gently inflated around a narrow umbilicus.

Septal sutures are partly exposed but not clearly traced.

**Comparison.**—At present only one specimen (holotype) is available for this species. Its approximate size described above is somewhat larger than the lectotype of *Turrilites acutus* Passy, 1832 (pl. 16, fig. 3; reillustrated by Wright and Kennedy, 1996, pl. 105, fig. 5) and probably smaller than the lectotype of *Turrilites wiestii* Sharpe, 1857 (pl. 27, fig. 8; reillustrated by Wright and Kennedy, 1996, pl. 105, fig. 18).

Some young shells of *Turrilites scheuchzerianus* Bosc, 1801, exemplified by such specimens as illustrated by Wright and Kennedy (1996, text-fig. 138C–D, F–G, N; pl. 107, fig. 1), are somewhat similar to the present species in

showing a downward broadening whorl, nodelike swelling, if not tuberculation, of the lower ribs, and the smooth basal surface. However, in typical examples of *T. scheuchzerianus* the apical angle is smaller, the whorl flank is gently convex, and the tubercles are not developed.

With respect to the characteristic whorl shape, the present species is similar to a certain form of *T. wiestii* represented by a group of specimens illustrated by Wright and Kennedy, 1996, pl. 105, figs. 7, 8, 11 and pl. 108, figs. 9, 13. It is, however, different from the above form as well as the lectotype of *T. wiestii* (Sharpe, 1857, pl. 27, fig. 8; reillustrated by Wright and Kennedy, 1996, pl. 105, fig. 18) in its more numerous and less distant ribs with weaker tubercles. The lectotype shows a dissimilar whorl shape.

This species could be referred to the subgenus *Ostlingoceras* (*Ostlingoceras*) Hyatt, 1900, but in the latter the transversal ribs are more numerous and crowded, the tubercles of the second row are smaller and weaker, and the lower (or basal) surface of the whorl has radial ribs, with third and/or fourth rows of small tubercles on its marginal zone. The ribs on the holotype of *T. miroku* are 22 per whorl, showing nearly the same density as that of *T. costatus* (see Tables 2 and 5).

**Discussion.**—This species is somewhat peculiar in its morphological characters. In this paper it is assigned at least tentatively to *Turrilites* on the grounds of the above comparison.

The holotype of this species was in a transported nodule, which can be inferred to have been derived from somewhere in the lower Cenomanian on account of its having been recovered close to Loc. 1k1065b, where a lower Cenomanian species, *Ostlingoceras* (*O.*) *bechei* (Sharpe) was obtained (see Matsumoto and Takahashi, 2000, p. 262). It should be noted that *T. wiestii* is recorded from the lower Cenomanian of England near the boundary of the *Mantelliceras dixonii* Zone and the *Acanthoceras rhotomagense* Zone (Wright and Kennedy, 1996, p. 354).

At any rate, we have to get more material to clear up questionable points about the systematic and biostratigraphic allocation of the present species.

#### Genus *Mesoturrilites* Breistroffer, 1953

**Type species.**—*Turrilites aumalensis* Coquand, 1862.

**Diagnosis.**—Turrilitid ammonoids with four rows of tubercles or ribs; the first row on the main part of flank made up of ribs and/or tubercles, the second and the third rows of small tubercles on spirally elongated, narrow ridges separated by a groove; the fourth row of small tubercles on the marginal zone of the lower whorl surface where radial ribs run to a narrow umbilicus (modified from Matsumoto and Inoma, 1999, p. 37).



***Mesoturritiles* cf. *aumalensis*** (Coquand, 1862)

Figure 3 N

**Compared.—***Turritiles aumalensis* Coquand, 1862, p. 323, pl. 35, fig. 3.*Mesoturritiles aumalensis* (Coquand, 1862). Wright and Kennedy, 1996, p. 346, pl. 98, fig. 5; pl. 105, figs. 2, 3, 14; text-figs. 134J, K; 138S-U, W; 146A-G (with full synonymy).

**Material.**—GK.H8562 [= previous GT.I-3310] (Figure 3N), collected by T. M. in 1938 at Loc. T591a, the lowest part of a sequence of strata exposed on the right side of the River Abeshinai in the Nakagawa district.

**Descriptive remarks.**—This specimen is small and incompletely preserved. It shows a pyramidal shape, conical tubercles of moderate intensity and density at about the midflank, and corresponding number of spirally elongated tubercles in two rows, with a narrow groove in between, along the lower whorl seam. The clavate tubercles of the fourth

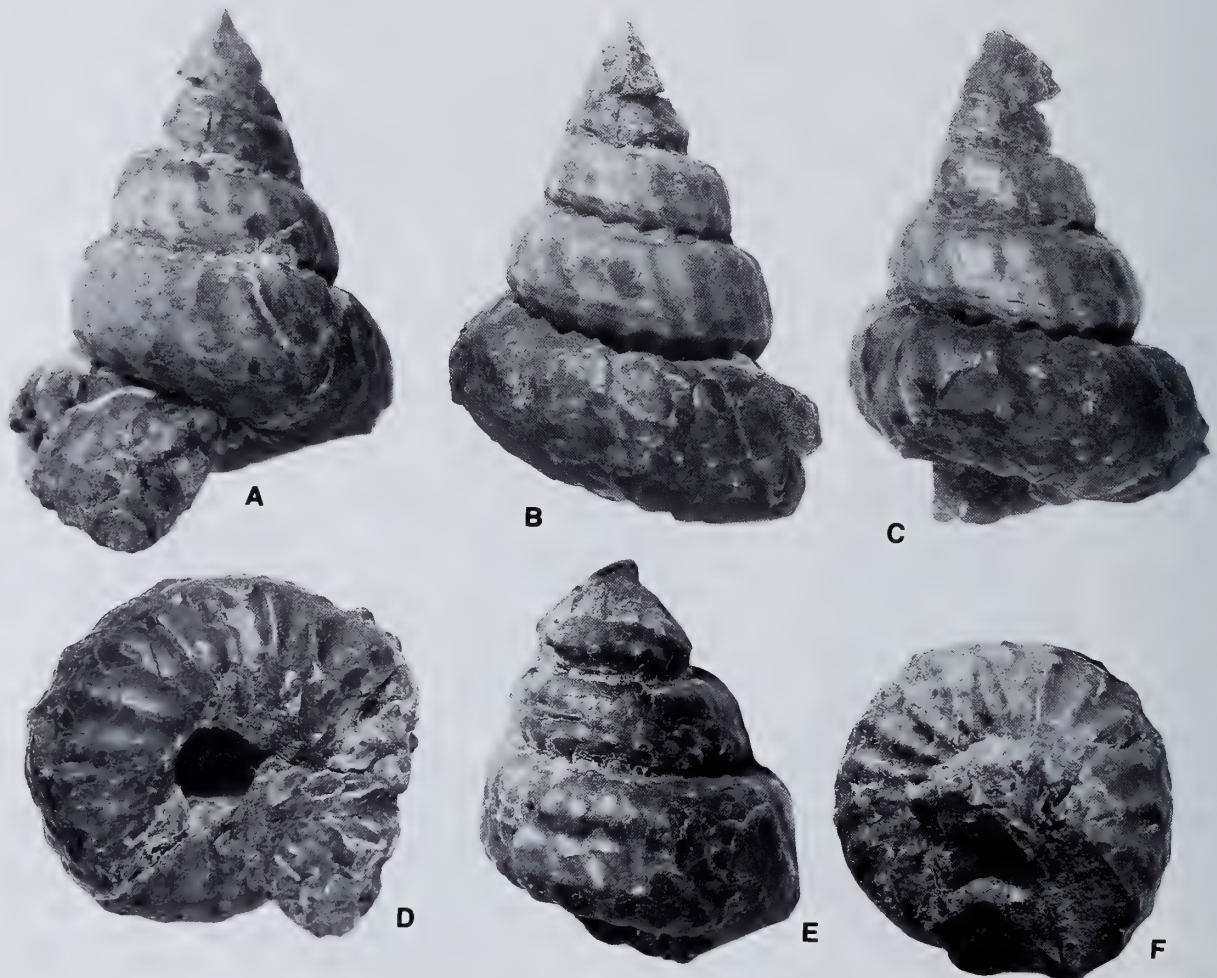
row and radial ribs arising from them are faintly discernible on the lower face. Although the preservation is insufficient, this specimen can be called *Mesoturritiles* cf. *aumalensis*. It occurs at the level immediately below that of *Turritiles complexus* (*vide ante*).

***Mesoturritiles pombetsensis* sp. nov.**

Figures 8, 9

**Material and occurrence.**—Holotype, here designated, is GK.H8532 [= previous S. 37·7·17] (Figure 8A–D) collected by T. T. in 1963 from a transported nodule on the Onkonosawa, a branch of the River Ponbetsu in the Mikasa district. Paratype is GK.H8548 (Figure 8E, F), collected by T. T. at Loc. Ik1101 on the right side of the R. Ikushunbetsu. The fossiliferous sandy rocks which contain the above specimens are referred to the lower part of the Member IIb of the Mikasa Formation.

**Diagnosis.**—Pyramid-shaped species of *Mesoturritiles*



**Figure 8.** A–F. *Mesoturritiles pombetsensis* sp. nov. Three lateral (A, B and C turned about 120° anticlockwise) and basal (D) views of GK.H8532 (holotype), slightly, over natural size. Lateral (E) and basal (F) views of GK.H8548,  $\times 1.67$ . Photos courtesy of M. Noda.



**Table 6.** Measurements of *Mesoturritilites pombetsensis* sp. nov.

Specimen	NW	Hp	Ht	D	ap	h	d	h/d	R(T)
GK.H8532	5.5	55.0	60.0	46.0	47°	14.7	33.7	0.44	18
GK.H8548	3.0	29.0	42.0	28.0	45°	8.3	19.3	0.43	22

Legend as for Table 1.

with moderate apical angle, ornamented by fairly coarse ribs on the upper flank, each of which is provided with a node at about the midflank immediately above a shallow concave zone; also two closely set rows of spirally elongate tubercles in the lower part with a groove in between. In more or less later stages the prorsiradiate ribs run across the concave zone and the groove. The ribs further extend radically on the gently convex lower (or basal) surface, with tubercles of the fourth row on the margin of the circular base.

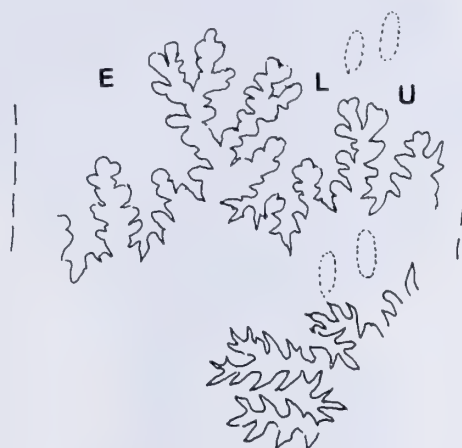
**Description.**—The holotype consists of nearly six septate whorls, with a fraction of crushed body chamber at the preserved end (Figure 8A, D). It is moderately large (Table 6). A single paratype is small and corresponds to the young part of the holotype. The entire shell shape is pyramidal; the exposed outer face of the whorl consists of a nearly flat or gently inclined upper portion, steeply inclined main part, and incurved lower portion. The interwhorl junction is deep.

The ornament somewhat changes with growth. In the early growth stage the upper ribs are very coarse and tuberculated at their lower end. This is well manifested at the early stage (with  $d < 15$  mm) of the paratype, but is less clear in the holotype. Below the zone of upper ribs a shallowly concave, spiral zone runs at about the midflank. In the middle to late growth stages, the ribs are elongated and the spiral groove is reduced. The prorsiradiate ribs run across the shallowing groove and connect themselves with the spirally elongated tubercles of the second and third rows. They extend to the radial ribs on the lower surface. The ribs are curved at about the rounded, small tubercles of the fourth row. On the well preserved lower face, delicate spiral lines or lirae may be observed and tiny dots may be discernible at the crossing points with the radial ribs (Figure 8 D, F).

Septal suture is deeply and finely indented. Moreover, the extra branches of a lobe (?) are extended from the other side (Figure 9).

**Comparison and discussion.**—The holotype of this species is the largest among hitherto reported specimens of *Mesoturritilites*. If its body chamber is preserved, it would be about 80 mm in height and 75 mm in basal diameter. However, it is actually difficult to estimate the real size of the adult shell in the previously described species, because their types are incompletely preserved.

The present species is somewhat allied to *Mesoturritilites aumalensis* (Coquand, 1862) (p. 323, pl. 35, fig. 3), redefined by Wright and Kennedy (1996, *vide ante*) in the general shell shape and the ornamentation of the young stage. In later growth stages ribs become predominant in the former, whereas tubercles characterize the latter. In this respect this species may be somewhat allied to *M. corrugatus* Wright and Kennedy (1996, p. 348, pl. 98, figs. 4, 17), but the ribs in the latter are narrower and sharper, without such



**Figure 9.** *Mesoturritilites pombetsensis* sp. nov. External suture of GK.H8532 (holotype) at  $h = 15$  mm. Figure is about  $\times 4$ . Symbols as for Figure 6. Drawing by T. M.

nodes as seen on the ribs of *M. pombetsensis*.

**Distribution.**—At present this species is represented by only two specimens from the lower part of the Cenomanian in Hokkaido. Although they are fairly well preserved, more material should be searched for to ascertain the vertical range and geographical distribution.

Genus *Mariella* Nowak, 1916

Subgenus *Mariella* (*Mariella*) Nowak, 1916

**Remarks.**—Altogether 10 species of *M. (Mariella)* from Hokkaido have been recently described (Matsumoto *et al.*, 1999; Matsumoto and Kawashita, 1999; Matsumoto and Kijima, 2000; Matsumoto *et al.*, 2000). Two more species are described below.

*Mariella (Mariella) cenomaniensis* (Schlüter, 1876)

Figure 10

**Type.**—Lectotype, by the subsequent designation of Kennedy, 1971 (p. 29), is the original of Schlüter, 1876, pl. 37, fig. 6. The specimen illustrated by Wright and Kennedy (1996, text-fig. 141B) is supposed to be this specimen.

**Material and occurrence.**—GK.H8557 [= previous S.55-9-14] (Figure 10A, B), collected by T. T. in 1960 at the point of the Hachigatsu-zawa, near the confluence with the branch rivulet called the Okufutamata-zawa. It is in a calcareous nodule of fine sandstone derived probably from the lower



**Figure 10.** *Mariella (Mariella) cenomanensis* (Schlüter, 1876). Lateral (A) and basal (B) views of GK.H8557,  $\times 1.5$ . Photos courtesy of M. Noda.

Cenomanian part exposed upstream from this locality (see the Geological Map of Kamiashibetsu by Shimizu *et al.*, 1953).

**Description.**—This single specimen is small but it shows 9 whorls. Its estimated apical angle is low (about  $20^\circ$ ), although it is somewhat deformed. The outer exposed whorl face is convex and the whorl junction is deeply impressed. The exposed part of each whorl in lateral view is comparatively high, showing  $h/d = 0.62$  in a measured part.

The tubercles in two rows on the main part of the flank are coarse, numbering 18 per whorl in each row. There is a smooth sloping zone above the upper row of subrounded tubercles. The tubercles of the second row are somewhat clavate. There are spirally elongated tubercles of the closely set third and fourth rows at about the edge between the lateral and lower (or basal) faces.

**Remarks.**—This specimen resembles smaller examples of *M. (M.) cenomanensis*, e. g., those described by Kennedy (1971, p. 28, pl. 8, fig. 10) and Atabekian (1985, p. 41, pl. 10, figs. 1–6). It is certainly identified with this species on the grounds of the described characters. The apical angle  $23^\circ$  by Wright and Kennedy (1996, p. 342) is somewhat larger than that in ours or in Atabekian's small specimens. This may depend on estimations made from the whorls of different growth stages.

**Distribution.**—*M. (M.) cenomanensis* has been reported to occur in the lower Cenomanian of various regions in the world (see Wright and Kennedy, 1996, p. 344).

***Mariella (Mariella) aff. circumtaeniata* (Kossmat, 1895)**

Figure 11

**Compared. —**

*Turritiles circumtaeniatus* Kossmat, 1895, p. 141, pl. 18, figs. 4, 5.

*Mariella (Mariella) circumtaeniata* (Kossmat, 1895). Klinger and Kennedy, 1978, p. 26, pl. 5, figs. A–C; text figs. 3G, 6D (with full synonymy)

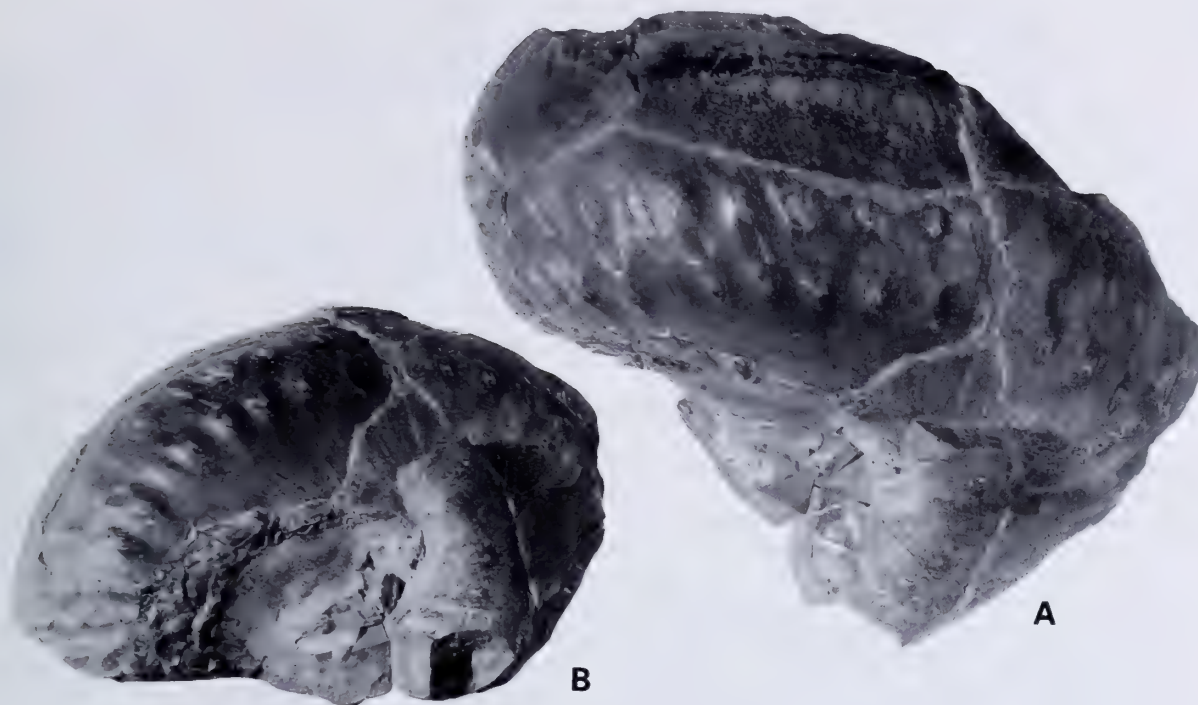
**Material.**—IGPS 108380 (Figure 11A, B), collected by Makoto Okamura in 1972, at his Loc. AB14 [= Loc. T590c of Matsumoto (1942)] on the left side of the River Abeshinai in the Nakagawa district.

**Descriptive remarks.**—This specimen is a highly distorted body chamber, measured as  $106 \times 50$  mm in the basal outline. The flank on the figured part (Figure 11A) is well rounded, but the other side is flattened. The ornament consists of three rows of tubercles and the looped ribs. The looping or intercalation of the ribs is frequent in the space between the upper row of tubercles and the upper whorl seam. The interval between the upper and middle rows of tubercles is slightly wider than that between the middle and lower rows. The coiling is sinistral and the ribs are prorsiradiate, extending to the radial ones on the basal surface.

The tubercles of the first row and the ribs of the upper part are very weak. Whether this is the original character or a secondary feature created by weathering is not clear. As the body chamber alone is available, we have to leave the present material in open nomenclature. More material should be searched for to clear up the classification.

*M. (Mariella) circumtaeniata* has been reported to occur in the upper Albian of southern India, Madagascar, South Africa (Zululand) and (?) New Zealand (see Klinger and Kennedy, 1978, p. 26). The locality of the present specimen is referred to the Unit IIa (lower part of the Cenomanian) in the Abeshinai Valley.





**Figure 11.** *Mariella* (*Mariella*) aff. *circumtaeniata* (Kossmat, 1895). Lateral (**A**) and basal (**B**) views of IGPS 108380 (a crushed body chamber). A is  $\times 1$  and B is  $\times 0.8$ . Photos courtesy of M. Noda.

### Conclusions

To conclude this paper the following results are summarized.

(1) Three well known species of worldwide distribution, *Turrilites scheuchzerianus* Bosc, *T. costatus* Lamarck and *T. acutus* Passy, occur in the middle Cenomanian of Japan.

(2) *Turrilites complexus* sp. nov. is established on several specimens from the Mikasa and Nakagawa districts of Hokkaido, which were previously misidentified with *T. costatus*. This new species shows in youth some features of *T. scheuchzerianus* and later those of *T. costatus*. It retains also some characters of *Mariella* (*Mariella*) *oehlerti* (Pervinquière).

(3) Another new species, *T. miroku*, based on a single specimen from Mikasa, is similar in some respects to a certain form of *T. wiestii* Sharpe, but distinct from the lectotype of the latter. Further study of more material is required.

(4) *Mesoturrilites* cf. *aumalensis* (Coquand) is found in the lower Cenomanian of Nakagawa. Furthermore, *M. pombetsensis* sp. nov. is erected on the specimens from the lower Cenomanian of Mikasa. It has distinct ribs and weaker tubercles.

(5) *Mariella* (*Mariella*) *cenomanensis* (Schlüter), another cosmopolitan, is first recorded from Hokkaido.

(6) *M. (M.)* aff. *circumtaeniata* (Kossmat) is reported from Nakagawa, but more material is required for adequate taxonomy and age correlation.

### Acknowledgments

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## Small Permian dicynodonts from India

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**Abstract.** The Lower Gondwana Kundaram Formation of the Pranhita-Godavari valley records the sole occurrence of Permian amniotes in India. The horizon has yielded various dicynodonts, mainly represented by medium-sized *Endothiodon*. This assemblage also contains several small dicynodonts belonging to the family Pristerodontidae and Emydopidae. *Pristerodon* (*P. mackayi* Huxley, 1868), *Emydops* (*E. platyceps* Broom and Haughton, 1917) and *Cistecephalus* (*C. microrhinus* Owen, 1876) are described here. This is the first detailed description of these genera from outside Africa. The older name *Emydops* in place of *Emydoses* is retained and the Indian specimens of *Pristerodon*, *Emydops* and *Cistecephalus* are compared with those from the Beaufort Group, Karoo Supergroup of South Africa. Based on its vertebrate fauna, the Kundaram Formation is broadly correlated with the *Tropidostoma* and *Cistecephalus* Assemblage Zones of the Beaufort Group, Karoo Supergroup, South Africa, the basal beds of the Madumabisa Mudstones of Zambia, the Ruhuhu and the lower part of the Kawinga Formation of Tanzania and the Morro Pelado Member of the Rio do Rasto Formation of Brazil. It suggests a Late Permian Tatarian age for the Kundaram Formation. The distribution of the Kundaram dicynodonts in the other Gondwanan countries indicates the close proximity of the continents during that period and a lack of endemism or provinciality.

**Key words:** Dicynodont, Gondwana, Kundaram, Pranhita-Godavari valley

### Introduction

Permian dicynodonts have been reported from the Kundaram Formation, a Lower Gondwana horizon of the Pranhita-Godavari valley, one of the several Gondwana basins in India (Kutty, 1972; Ray, 1997). The formation is underlain by the coal-bearing Barakar Formation and overlain by the sand-dominant Kamthi Formation (Table 1). The fluvial sediments of the Kundaram Formation comprise red mudstone, sandstone, sandstone-mudstone alternations and ferruginous shale (Ray, 1997).

The extensive red mudstone ground of the Kundaram Formation contains abundant fossils of Permian dicynodonts, which have been collected from the two localities near Golet (Figure 1) in the northwestern part of the Pranhita-Godavari valley (Kutty, 1972). Most of the specimens were encrusted with a hard iron matrix, resulting in the masking of the original shapes and forming oblate and spherical nodules. These were collected *in situ* as isolated skulls with and without lower jaws and other cranial fragments. The separated skulls and lower jaws are mainly preserved with their dorsal sides up. Those skulls with associated lower jaws are found lying on their sides with their lateral sides up. Postcranial elements are relatively rare though a few in the form of rolled vertebrae and broken limb

ends are present and show signs of rolling, abrasion and rounding.

Fossil material prepared mechanically with a dental vibrotome reveals the preponderance of medium-sized *Endothiodon* (superfamily Endothiodontoidea). There are at present two species of *Endothiodon*, *E. uniseries* and *E. mahalanobisi* (Ray, 2000). The former has a skull length (SL) around 300 mm while in the latter it is around 160 mm. In addition, the assemblage contains some very small dicynodonts (SL 50 mm approx.) characterised by a broad intertemporal bar relative to the interorbital region. The aim of this paper is to describe the small and varied dicynodonts of the Kundaram Formation. These dicynodonts are known mainly from Africa and those mentioned here are the first forms from outside Africa to be described in detail. The paper also discusses the biostratigraphic and palaeobiogeographic implications of this unique fauna.

### Systematic palaeontology

Infraorder Dicynodontia Owen, 1859  
Superfamily Pristerodontoidea Cluver and King, 1983  
Family Pristerodontidae King, 1988  
Genus *Pristerodon* Huxley, 1868

**Table 1.** Lower Gondwana succession of the Pranhita-Godavari valley, India.

Formations	Main lithologies	Fossils	Age
Kamthi	Sandstone and siltstone	?dicynodont	Permo-Triassic
Kundaram	Mudstone, sandstone and ferruginous shale	dicynodonts, captorhinid	Late Permian
Barakar	Sandstone, carbonaceous shale and coal	<i>Glossopteris</i> flora	Early to Late Permian
Talchir	Tillite, greenish shale, sandstone		Early Permian

*Type species.*—*Pristerodon mackayi* Huxley, 1868 (subsequent designation by Keyser, 1993).

***Pristerodon mackayi* Huxley, 1868**

Figures 2A–E, 3–4

*Pristerodon mackayi* Huxley, 1868, p. 204–205, pl. 12; King, 1988, p. 113; Keyser, 1993, p. 47 (see for prior synonymies).

*Holotype.*—BMNH R1810, skull and lower jaw from East

London, Cape Province, South Africa; *Cistecephalus* Assemblage Zone, Late Permian.

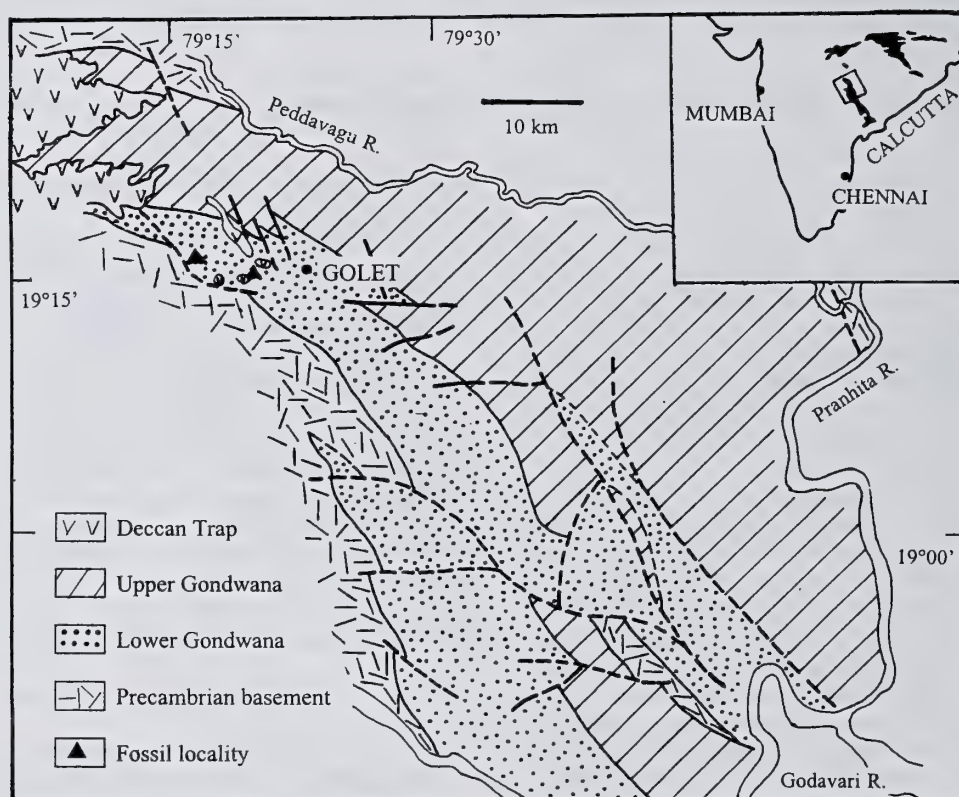
*Diagnosis.*—Small dicynodonts with or without maxillary tusks; broad intertemporal region; wide parietal exposure; palatine large, leaf-like; postcanine teeth in an oblique, anteriorly converging row; long interpterygoid vacuity extending to the rear of the vomer; median interpterygoid ridge continues anteriorly on the ventral surface of the anterior pterygoid process; deep dentary sulcus, prominent lateral dentary shelf (Cluver and King, 1983; King, 1988; Keyser, 1993).

*Material.*—ISIR 209, anterior part of a laterally compressed skull and lower jaw; ISIR 369, anterior part of skull; ISIR 370, distorted skull with lower jaw, ISIR 372, occiput.

*Repository.*—The specimens are housed in the Geology Museum, Indian Statistical Institute, Calcutta.

*Locality and horizon.*—Near Golet, Pranhita-Godavari valley, India; Kundaram Formation, Late Permian.

*Description.*—The Indian material includes a well preserved but laterally compressed, small, anterior half of a skull with associated lower jaw (ISIR 209). Its total length measured along the dorsal midline is inferred to be about 50.6 mm. The morphology of the skull and lower jaw follows the typical dicynodont pattern and the description of individual bones is not repeated here.

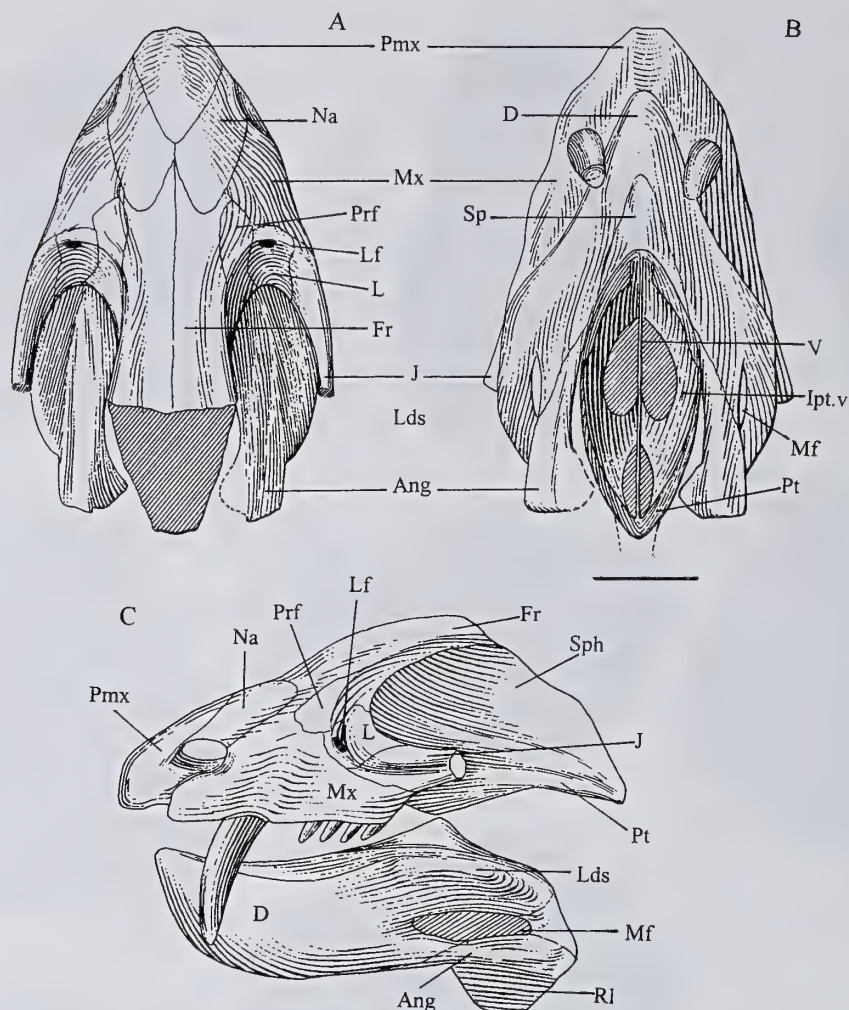


**Figure 1.** Geological map of the Pranhita-Godavari valley, India (after Kutty *et al.*, 1987) showing the fossil localities. Inset: Major Gondwana basins of India.

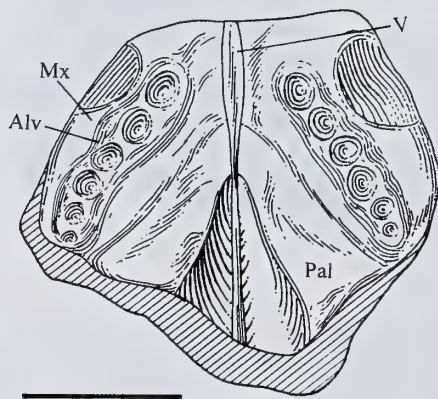




**Figure 2.** A-E. *Pristerodon mackayi* Huxley, 1868. A D. ISIR 209. Partial skull with attached lower jaw in A, dorsal, B, ventral, C, right lateral, D, left lateral views.  $\times 1.1$ . E. ISIR 372. Partial occiput in posterior view.  $\times 1.3$ . F-H. *Emydops platyceps* Broom and Haughton, 1917. ISIR 208. Skull and lower jaw in F, dorsal, G, ventral, H, right lateral views.  $\times 1$ . I-J. *Cistecephalus microrhinus* Owen 1876. ISIR 210. Partial skull and lower jaw in I, dorsal view.  $\times 1.3$ . J, left lateral view.  $\times 0.8$ .



**Figure 3.** *Pristerodon mackayi* Huxley, 1868. ISIR 209. Restored partial skull and lower jaw in **A**, dorsal, **B**, ventral and **C**, lateral views. Hatched lines indicate broken surfaces. Scale bar represents 10 mm.



**Figure 4.** *Pristerodon mackayi* Huxley, 1868. ISIR 369. Anterior part of skull in ventral view. Scale bar represents 10 mm.

### Skull

**Snout and skull roof.** The narrow and tapering snout is composed of the completely fused premaxillae, which continue posteriorly to form a wedge between the external nares. The nares open near the extremity of the snout. Small, subrounded septomaxilla, recessed within the naris, forms its posteroventral margin. The maxilla occupies the anterolateral sides of the skull and bears large caniniform tusks and about 3-4 postcanine teeth. The preorbital length (measured from the tip of the snout to the anterior end of orbit) is 16.6 mm. It is covered by the elongated, paired nasals mostly, followed by the frontals posteriorly. Only the anterior part of the orbit is preserved, well defined by a narrow rim. The preserved part of the interorbital region is broad (9 mm), flat and formed by the relatively extensive frontal. Anterolaterally the orbital rim consists of the subtriangular prefrontal, which is rather large in comparison to the more ventrally placed subrounded lacrimal and slender jugal. The lacrimal bears a prominent foramen just



flush with the orbital rim.

**Palate.** Palatal features are studied from ISIR 369 and ISIR 372 along with ISIR 209 as in the latter the lower jaw is in position. The anteriormost premaxilla forms a sharp peripheral rim and posteriorly is in sutural contact with the vomer medially and palatine and maxilla laterally. Posteromedial to the caniniform tusk in ISIR 209 or to the subcircular alveolus in ISIR 369, the maxilla bears a uniserial, short tooth row, tending to converge anteriorly. Though teeth are not preserved in ISIR 369, the apertures of the alveoli are confluent and form a short, shallow groove. The margin of this groove is raised above the surface of the maxilla. The palatines in ISIR 369 are broad, leaf-shaped, bearing undulations and forming the lateral margin of the choanal slits. The anterior pterygoid rami have sharp ventral edges (ISIR 209). In ISIR 372, the parasphenoid-basisphenoid complex as in other dicynodonts is fused to the posterior end of the pterygoid plate. The basisphenoid tubera are separated by a deep median cleft. Two distinct ridges run along the anterior surface of the tubera while their faces are laterally oriented, concave and consist of the foramen ovalis. In ISIR 209, the cultriform process of the parasphenoid extends as a slender rostrum between the interpterygoid vacuity. Anteriorly the sphenethmoid complex stands in a groove on the dorsal surface of the cultriform process.

The epipterygoid is L-shaped with a short anterior and longer posterior quadrate ramus. The quadrate-quadratojugal complex is typical of dicynodonts.

**Occipital and otic regions.** In ISIR 372, the occiput is subrectangular in shape and is flanked on either side by the squamosal. The occipital condyle is situated medially almost near its ventral margin. Above the condyle is situated an elongate foramen magnum. A major portion of the occiput is formed by the large, medially placed supraoccipital ventrally and interparietal dorsally. Laterally the supraoccipital is in sutural contact with the tabulars and ventrolaterally with the rodlike opisthotic. This latter suture is interrupted by a distinct post-temporal fenestra. The opisthotic forms the ventral margin of the occiput. Laterally on either side of the condyle is a pair of jugular foramen, piercing the exoccipitals.

### Lower jaw

The portion of the lower jaw anterior to the Meckelian fenestra is preserved in ISIR 209. The relationships of the various elements of the lower jaw follow the normal dicynodont pattern. The anterior dentary symphyseal end is narrow, slender and forms a cutting edge. Though the dorsal surface is hardly visible as the lower jaw is attached to the skull, a deep but short, longitudinal dentary sulcus is discerned, which is for occlusion with the upper jaw teeth. Laterally the jaw ramus bears a distinct and high dentary shelf just above and anterodorsal to the Meckelian fenestra, which is quite long and elliptical. The dentary extends up to the posterodorsal end of the fenestra while the angular forms its ventral margin. The subrounded reflected lamina of the angular extends well below the ventral margin of the lower jaw. A small, elongated splenial medially forms the anteroventral margin of the lower jaw. The anterior end of

the rodlike prearticular is preserved and in sutural contact with the splenial.

**Discussion.**—An imperfect 'lacertilian' skull collected by G. Mackay from East London, South Africa was originally described by Huxley (1868) as *Pristerodon mackayi*. It was a nearly complete skull with a posteriorly widening intertemporal bar. The skull was considered by Seeley (1895) to be an endothiodont because of its postcanine teeth. Many diverse dicynodonts bearing little or no resemblance to each other except for the postcanine teeth were traditionally placed under Endothiodontidae. Later works by Van Hoepen (1934) and Cluver and King (1983) led to the placement of *Pristerodon* and its related forms within the family Pristerodontidae. King and Rubidge (1993) considered *Pristerodon* to be characterised by a broad intertemporal bar with exposed parietals, large, leaflike palatine, postcanine teeth in a short oblique row, long interpterygoid vacuity, deep dentary sulcus and a prominent lateral dentary shelf. All the *Pristerodon* species (*P. mackayi*, *P. agilis*, *P. boonstrai*, *P. buffaloensis*, *P. vanhoepeni* and *P. whaitsi*) were differentiated on the bases of the presence or absence of the maxillary tusk, nasal bosses and position of the alveolus (King, 1988).

However, investigation of a large number of toothed dicynodonts earlier considered as endothiodont by Keyser (1993) revealed that the vast majority of the described species belonging to *Pristerodon* and various other genera are junior synonyms of *Pristerodon mackayi*, the only valid species of *Pristerodon*. He further suggested that the crista oesophagea forming ridges on the anterior pterygoid rami is a diagnostic feature of *Pristerodon*. On the other hand, King and Rubidge (1993) emphasised the sigmoidal curve of the anterior pterygoid ramus of *Pristerodon*.

All the Indian specimens (ISIR 209, ISIR 369, ISIR 370, ISIR 372) are skulls of small dicynodonts with an average skull length of about 50 mm. These are characterised by caniniform tusks, wide intertemporal regions, short, oblique postcanine tooth row, large, leaflike palatines, high and distinct lateral dentary shelf and deep dentary sulcus. All these features definitely show that these pertain to *Pristerodon mackayi*.

Superfamily Diictodontoidea Cluver and King, 1983

Family Emydopidae Cluver and King, 1983

Subfamily Emydopinae Cluver and King, 1983

Genus *Emydops* Broom, 1912

**Type species.**—*Emydops minor* Broom, 1912 (subsequent designation by Keyser, 1993).

*Emydops platyceps* Broom and Haughton, 1917

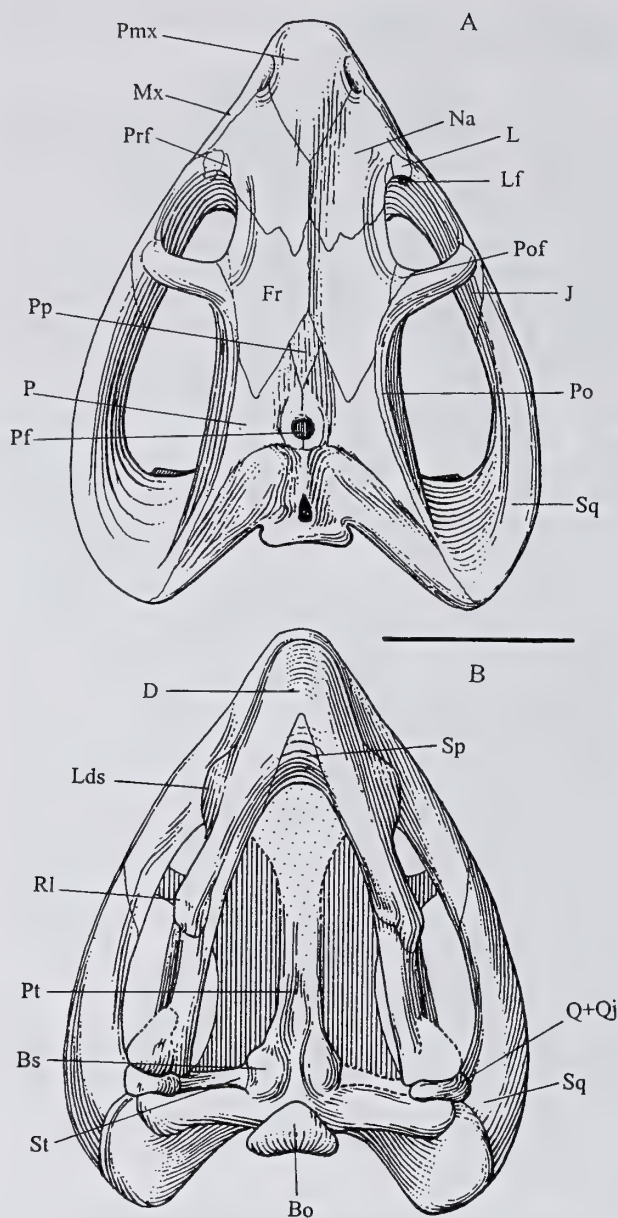
Figures 2F-H, 5-6, 7E-F

*Emydops platyceps* Broom and Haughton, 1917, p. 125; King, 1988, p. 116.

*Emydops tener* Keyser, 1993, p. 49, fig. 5.1.

**Holotype.**—SAM-PK-2667, skull from Dunedin, Beaufort West, South Africa; *Cistecephalus* Assemblage Zone, Late Permian.

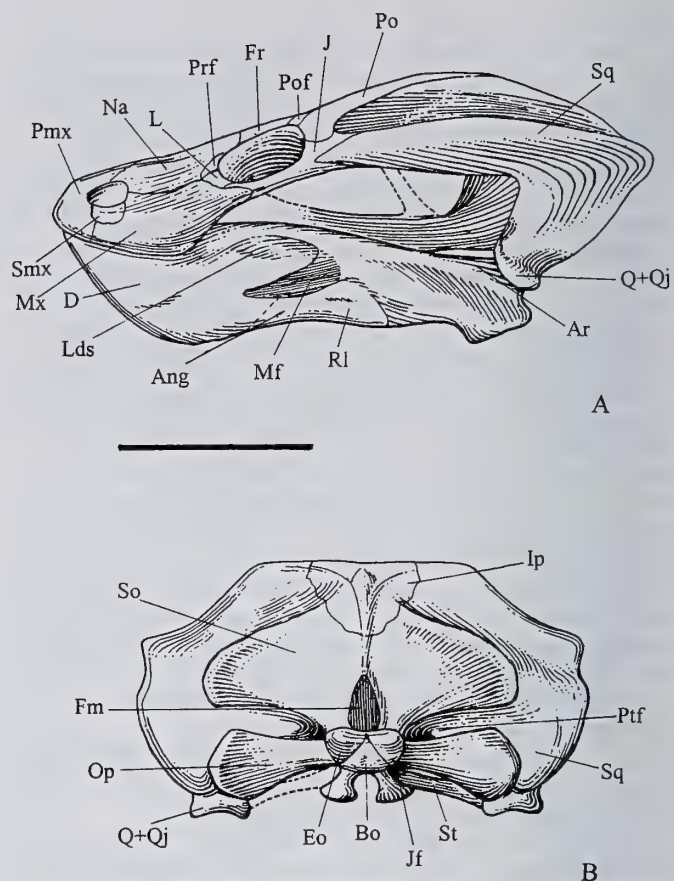




**Figure 5.** *Emydops platyceps* Broom and Houghton, 1917. ISIR 208. Restored skull and lower jaw in **A**, dorsal and **B**, ventral views. The stippled area indicates matrix covering. Scale bar represents 20 mm.

**Revised diagnosis.**—Small dicynodonts with or without caniniform tusks; prominent lacrimal foramen; wide intertemporal region with parietal exposure; median premaxillary ridge on palate bordered by grooves on either side, irregularly placed maxillary and dentary teeth; small palatal embayment just anterior to caniniform process; flat, squarish palatine with notched medial and concave posterior margins; straight anterior pterygoid process, prominent lateral dentary shelf; dentary symphysis drawn up into a sharp cutting edge.

**Material.**—ISIR 208, a complete, slightly distorted skull



**Figure 6.** *Emydops platyceps* Broom and Houghton, 1917. ISIR 208. Restored skull and lower jaw in **A**, lateral and **B**, occipital views. Scale bar represents 20 mm.

with attached lower jaw.

**Repository.**—The specimen is housed in the Geology Museum, Indian Statistical Institute, Calcutta.

**Locality and horizon.**—The specimens were collected near Golet (Figure 1), Adilabad district, Andhra Pradesh, India from the Late Permian Kundaram Formation, Gondwana Supergroup.

**Description.**—

### Skull

**General features.** The small and triangular skull measures 47.8 mm along the dorsal midline. The snout is narrow, tapering anteriorly and quite short (preorbital length is 10 mm). Measurements of the skull are given in Table 2. The elliptical nostril is situated close to the midline at the extremity of the snout. It is bordered by the premaxilla anterodorsally, nasals posterodorsally and the maxilla posteriorly and ventrally. The orbit is relatively small, subrounded (diameter 10 mm approx.) and anterodorsally positioned. The interorbital region is flat, quite broad and about 15.5 mm. Beyond the orbit, the zygomatic arch flares out and meets the occipital plane at a high angle. The temporal fenestra is large, elongated and extended beyond the level of the occipital condyle. The intertemporal region is much wider than the



**Table 2.** Measurements of the skull (ISIR 208) of *Emydops platyceps*. All measured in mm.

Parameters	<i>Emydops platyceps</i> (ISIR 208)
Skull length	
a. Measured along the dorsal midline	47.8
b. Over squamosal wings	58.4
c. At palatal midline	—
Preorbital snout length	10
Postorbital snout length	25
Length from anterior edge of premaxilla to anterior edge of pineal foramen	37
Skull width across squamosal	44.5
Diameter of pineal foramen	2.8
Interorbital width	15.5
Intertemporal width	28
Snout width	16.7
Length of temporal fenestra	31.6
Width of temporal fenestra	14.3
Greatest width of occiput	41.3
Width of occipital condyle	13.8
Least squamosal width of the occiput	28
Occipital height	25.5

interorbital bar (Table 2) and gradually widens posteriorly. A small, circular pineal foramen is situated medially on a slightly raised area at the posterior end of the skull. The skull roof is relatively flat but gently sloping anteriorly. The occiput is trapezoid in shape with a large, elliptical occipital condyle situated medially near its ventral margin.

**Snout and skull roof.** The anteriormost premaxilla separates the nostrils dorsally and forms a wedge-shaped contact with the paired nasals posteriorly. Posterolaterally it is in contact with the maxilla, a major element on the anterolateral sides of the skull. The maxilla borders the nasal openings ventrally and posteriorly. The septomaxilla is slightly exposed along the posteroventral border of the nasal cavity. In dorsal view, posterior to the premaxilla is a pair of large nasals. This is followed posteriorly by the frontal occupying most of the skull roof anterior to the temporal fenestra. Posterolaterally the nasal is bordered by a small elongated prefrontal. The latter, along with the relatively large, subrounded lacrimal, form the anterior margin of the orbit. There is a distinct lacrimal foramen. Dorsally and posterodorsally the circumorbital rim is formed by the frontal and a small, triangular postfrontal respectively. Ventrally the orbit is bordered by the jugal. The slender, rodlike postorbital forms the narrow anteromedial border of the temporal fenestra. Characteristically the intertemporal region comprises mostly the widely exposed parietals. Medially at the frontoparietal junction is a large, rhomboidal preparietal, which lies entirely in front of the pineal foramen. The circular pineal foramen is situated on a slightly raised area, at the posterior end of the skull roof and is bounded by the parie-

tals. Posterior to the pineal foramen is a single, large interparietal, which occupies a dorsomedial position on the occiput. The squamosal is the posteriormost element in dorsal view and divisible into three parts as is typical of dicynodonts. Attached to the anterior face of the squamosal is a small quadratojugal.

**Palate.** The anterior part of the palate cannot be partly seen because of matrix covering and as the lower jaw is in position. Posteriorly the pterygoid bone is narrow with a poorly developed pterygoid crest.

The parasphenoid-basisphenoid complex is fused to the posterior end of the pterygoid plate. The basisphenoid consists of two anteriorly converging tubera separated by a narrow and deep median cleft. The faces of the tubera are laterally oriented, concave and house the foramen ovalis.

The quadrate is strongly fused with the more laterally placed quadratojugal, though there is deep groove between them. The palatal face of the quadrate, as in other dicynodonts, is composed of a broad, medial and a lateral condyle separated by a shallow groove. Lying between the medial face of the quadrate and the fenestra ovalis is a thin, long, rodlike, imperforate stapes with slightly expanded ends.

**Occipital and otic regions.** In posterior view, the occiput is trapezoid in outline. It bears a prominent, elliptical occipital condyle medially, which is composed of the paired exoccipitals and the basioccipital. Above the condyle is an elongated, triangular foramen magnum. The dorsal margin of the foramen magnum is formed by the supraoccipital, which also forms the roof of the braincase. The interparietal, situated on the dorsal side of the supraoccipital, is characterised by a median ridge tapering ventrally. Ventrolateral to the condyle is a jugular foramen, piercing the exoccipital and the rodlike opisthotic, which expand laterally overlapping the squamosal. A large post-temporal fenestra is present near the occipital condyle at the sutural contact between the opisthotic and the dorsally placed supraoccipital. Laterally the occiput is margined by the winglike flanges of the squamosal. The anterior face of the occiput bears a pair of small, flat prootics, which along with the opisthotics form the anterior and posterior walls, respectively of the otic capsule.

### Lower jaw

The lower jaw is attached to the skull. The anterior end is relatively slender and is drawn up into a sharp cutting edge. The dentary symphysis is strongly fused. Laterally the jaw ramus bears a distinct, high dentary shelf and a large Meckelian fenestra. The anteriormost element of the lower jaw, the dentary, extends posteriorly as far as the posterior end of the Meckelian fenestra. It is bounded posteriorly by the surangular and posteroventrally by the angular. Presence or absence of teeth cannot be determined as the lower jaw is in position. The reflected lamina of the angular is quite small and is in line with the ventral margin of the lower jaw. The transversely widened posterodorsal surface of the articular forms lateral and medial condyles separated by a low ridge as found in the dicynodonts. It slopes downward posteriorly to form the retroarticular process.

*Discussion.*—



### On the genus *Emydops*

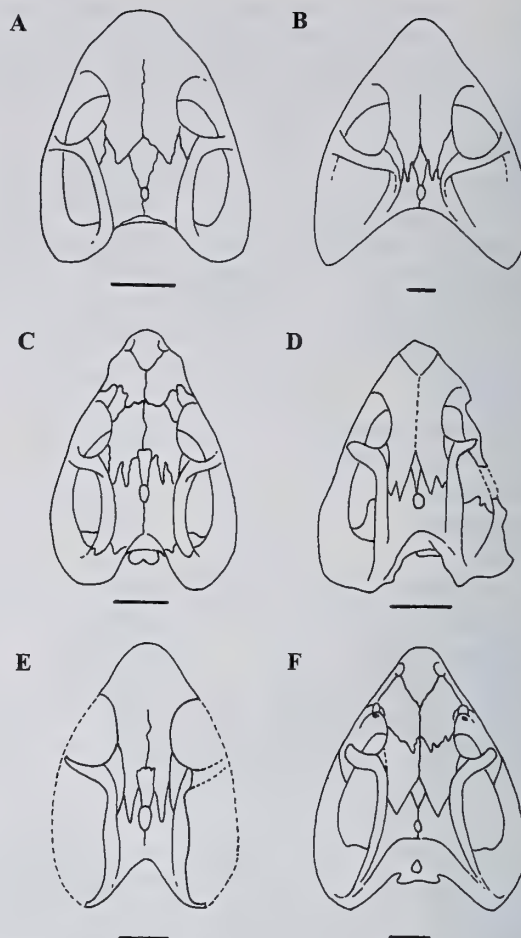
A small dicynodont skull, about 45 mm in length, was first described by Broom (1912) from Kuilspoort, Beaufort West, South Africa as a new genus and species *Emydops minor*. It is tuskless with a wide intertemporal region, a large median preparietal forming the anterior margin of the pineal foramen, a slender postorbital arch and a feeble beak. Broom (1913) redefined *Emydops* as a small tuskless form with a few unserrated postcanine teeth. Subsequently, a number of *Emydops* species, collected from the Permian part of the Beaufort Group of South Africa, were described by Broom (1913, 1921). These species were distinguished based on the shapes and arrangements of the bones of the frontal and parietal regions. Broom and Haughton (1917) described another new species of *Emydops*, *E. platyceps* based on a tusked skull from Dunedin, Beaufort West, South Africa.

Broom (1921) created a new genus *Emydopsis* (the type species is *Emydopsis trigoniceps*), characterised by the presence of only three or four posteriorly serrated teeth. Toerien (1953) stated that the number and size of the teeth alone cannot be used to differentiate between *Emydops*, *Emydopsis* and *Pristerodon*, then considered to be closely related to the former two genera. He further concluded that *Emydops* may be differentiated from *Pristerodon* on the basis of the size of the palatine and the absence of the palato-premaxillary contact in *Pristerodon*.

The holotypes of the type species of *Emydops*, *E. minor* (AMNH 5525; Figure 7A) and *Pristerodon*, *P. mackayi* (BMNHR 1810; Figure 7B) were again examined by Cluver and King (1983). They stated that in both specimens, few characters of taxonomic importance are visible. They supplemented the generic diagnoses of *Emydops* and *Pristerodon* from the information accumulated from other species of the two genera. According to them, the characteristic features of *Emydops* include: small dicynodonts with wide intertemporal region and exposed parietals (Figure 7C), platelike palatine with concave posterior border, quite short interpterygoidal vacuity, presence of embayment in the palatal rim and weak interpterygoidal crest, prominent lateral dentary shelf, dentary symphysis drawn up into sharp cutting edge and shallow groove on the dorsal edge of the dentary.

Keyser (1993) while reviewing the small dicynodonts of South Africa transferred most of the holotypes of *Emydops* species to *Pristerodon mackayi*. According to him, *Emydops minor*, the type species of *Emydops*, displays no distinctive features—a view also shared by Cluver and King (1983). Keyser (1993) found *E. minor* to be similar to *Pristerodon mackayi* and considered *Emydops minor* as *nomen dubium*. He suggested that *E. platyceps* is the only valid species, characterised by large and square palatines which are perforated by foramina. He renamed *Emydops* in part as *Emydoses* (Keyser, 1993, p. 48) and assigned two species to the genus, namely *Emydoses tener* (Figure 7D) and *Emydoses platyceps* (*Emydops platyceps* of Broom and Haughton, 1917; holotype SAM-PK-2667; Figure 7E).

However, King and Rubidge (1993) considered *Emydops* to be well characterised. *Emydops* is differentiated from the other toothed dicynodonts (*Eodicynodon*, *Pristerodon* and *Robertia*), based on such features of the palate and lower



**Figure 7.** Skulls in dorsal view. **A.** *Emydops minor*, holotype AMNH 5525 (after Cluver & King, 1983). **B.** *Pristerodon mackayi*, holotype BMNHR 1810 (after Cluver and King, 1983). **C–F.** *Emydops platyceps*, **C**, SAM-PK-11060 (after Cluver & King 1983); **D**, SAM-PK-K10170 (syntype, *Emydoses tener* of Keyser, 1993); **E**, holotype SAM-PK-2667, **F**, ISIR 208. Scale bars represent 10 mm.

jaw as the size and shape of the palatine, arrangement of the postcanine teeth, lateral dentary shelf and dorsal surface of the lower jaw (King and Rubidge, 1993; p. 141, table 2).

From the above review, it is evident that a disagreement persists regarding the nomenclature of the genus *Emydops*. Though Keyser (1993) in effect renamed *Emydops* as *Emydoses* because most of the earlier described species, including the type species of the formers, had in his view become junior synonyms of *Pristerodon mackayi*, the generic diagnosis remains nearly the same for *Emydops* and *Emydoses*. Moreover, *Emydops* is a long-accepted name in its accustomed meaning. Thus in the present study priority is given to the older name of the genus and the name *Emydops* is retained, to provide stability and avoid confusion in the nomenclature by introducing a new name.

### On the species of *Emydops*

As mentioned earlier Keyser (1993) considered *E.*



## Erratum

In the article by Komatsu, Saito and Fürsich (Vol. 5, No. 2), the columnar section in the upper left of Figure 7 (page 128) was partly obliterated during the printing process. Remove the corrected columnar section below and affix it to the appropriate position.

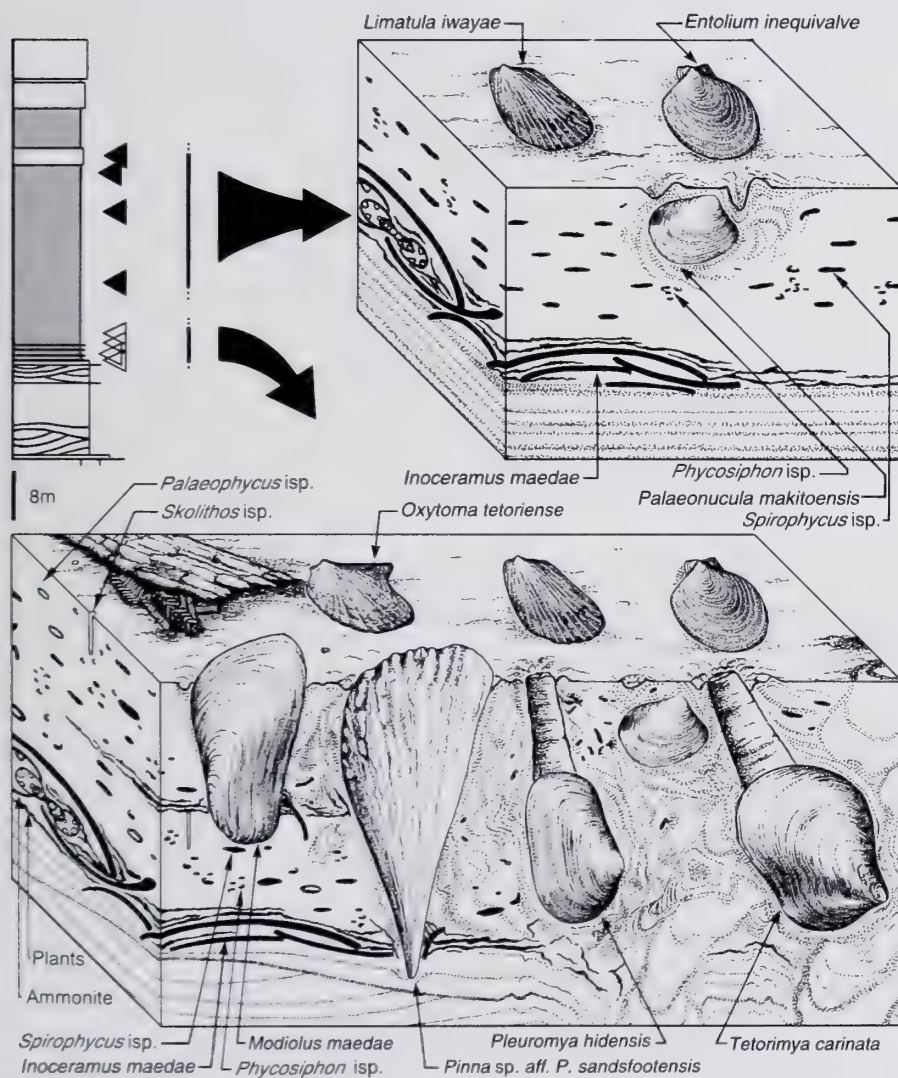
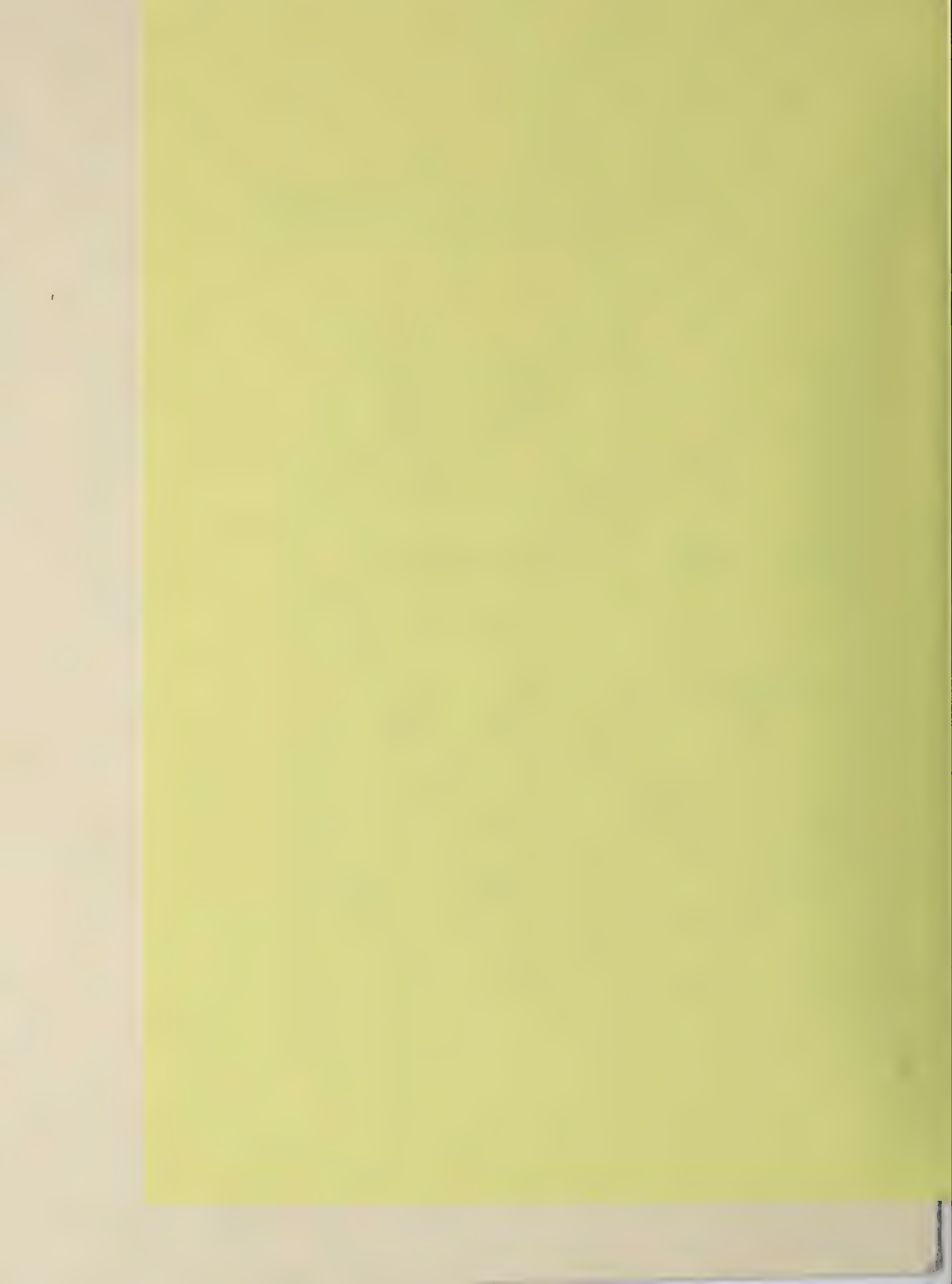


Figure 7. Ecological reconstruction of the bivalve fauna in shelf deposits of the Mitarai Formation.





**Table 3.** Comparative measurements of several specimens of *Emydops*. All measured in mm. Abbreviations used: SL, skull length along dorsal midline; SLsq, skull length over the squamosals; PSL, preorbital snout length; SnW, snout width; IO, interorbital width; IT, intertemporal width; TF, length of temporal fenestra; SW, skull width; OcH, occipital height; OcW, occipital width.

Specimens	Parameters										
	SL	SL sq	PSL	SnW	IO	IT	IT/IO	TF	SW	OcH	OcW
ISIR 208	47.8	58.4	10	16.7	15.5	28	1.81	31.6	44.5	25.5	41.3
SAM-PK-2667	40.58	51.9	9.75	15.68	10.69	15.69	1.48	-	34.54	-	-
SAM-PK-10170	49.33	61.36	7.97	17	10.52	19.88	1.89	32.9	47.46	18.35	39.58
SAM-PK-10148	51.06	58.72	16.26	16.28	10.96	18.38	1.68	30.2	42.88	23.66	35.34
SAM-PK-K1671	30.38	39.37	7.58	12.34	4.9	9.8	2	20.55	29.1	15.74	21.95
SAM-PK-3721	44	54.1	-	12.15	11.2	15.85	1.42	29.44	-	18.89	30.4
SAM-PK-10172	40.16	46.03	11.34	10.33	8.11	14.8	1.82	-	33.3	-	-
SAM-PK-11060	41.23	47.32	11.13	-	12	15.86	1.32	21	28.96	20.38	27.78
SAM-PK-K1517	46.69	56.64	11.58	-	15.38	19.77	1.3	17.5	30.4	22.03	30.6
SAM-PK-K5974	56.2	65.5	-	-	14.95	22.63	1.51	35.94	43.83	27	48.8
SAM-PK-K6693	47.94	59.56	12.33	16.37	12.08	18.54	1.53	25.7	44.4	18.85	33.22
SAM-PK-K6623	46.03	54.85	12.21	16.98	13.52	16.55	1.22	30.46	53.88	24.5	33.31

*platyceps* Broom and Haughton, 1917 and *E. tener* Keyser, 1993 as the only valid species. The former was characterised by large, squarish palatines, which are perforated by foramina and the latter by its "slender" build (Keyser 1993). The use of features like slender or delicate skull to define species is subjective (King, 1993) and avoided in the present study. A close examination of *Emydops* specimens housed at the South African Museum, Cape Town, including the holotype SAM-PK-2667 of *E. platyceps* and the syntypes (SAM-PK-10148 and SAM-PK-10170) of *E. tener* reveal that the shape of the palatines are similar in all the specimens. The palatal portion of the palatine is flat, squarish and bears a notch or palatine foramen in its medial margin. Its posterior margin is concave. Although the area between the medial margin of the palatine and the vomer along the ventral midline is covered with matrix in most of the specimens, the presence of the notch can be clearly discerned, especially in SAM-PK-10148, SAM-PK-3721, SAM-PK-K1671, SAM-PK-11060 and SAM-PK-K6623. Moreover, it appears that the syntypes of *E. tener* do not have any feature different from *E. platyceps* Broom and Haughton, 1917. It is considered here as the junior synonym of *E. platyceps* Broom, 1912. Thus, from the specimens available for study, it appears that the genus *Emydops* has only one valid species, *E. platyceps* and is now distinguished by the generic features of *Emydops*: small dicynodonts which may be tuskless or tuskless, prominent lacrimal foramen flush with the orbit, wide intertemporal region with broad parietal exposure, irregularly placed maxillary and dentary teeth, small embayment on the palatal rim anterior to the caniniform process, premaxillary ridge bordered by grooves on either side, flat, squarish palatine with notched medial and concave posterior margins, straight anterior pterygoid process, dentary symphysis drawn up into a sharp cutting edge and a prominent lateral dentary shelf.

#### Comparison between the Indian and South African forms

ISIR 208 (Figure 7F) is a small skull (47.8 mm) with broad intertemporal region and widely exposed parietal. The pterygoid bridge posterior to the choanae, though not well preserved, is quite narrow (Figure 5B). The lateral dentary shelf is very distinct and high and the dentary symphysis is drawn up into a sharp cutting edge. Thus, it is assigned to the genus *Emydops*. The anterior palatal features are not visible because of the position of the lower jaw. Table 3 gives a detailed comparison of ISIR 208 with a number of South African forms, including the holotype of *E. platyceps* (SAM-PK-2667), based on different cranial parameters. It shows that the overall skull proportions of ISIR 208 such as length, width, occipital height, occipital width and length of the temporal fenestra fall within the range of the South African forms. On the other hand, the snout length is much shorter while the interorbital and intertemporal width with respect to the skull length is much greater than that of the SAM specimens. IT/IO ratio (1.8) though again within the range, which varies from 1.22 (SAM-PK-K6623) and 2 (SAM-PK-3721), is at the higher end of the range. The interorbital (IO) and intertemporal (IT) width relative to the skull length and IT/IO ratio are found to be not reliable specific characters (Keyser, 1975; King, 1993) and are not considered here. However, in ISIR 208 the pineal foramen is situated near the end of the intertemporal bar. The preparietal lies entirely in front of the pineal foramen and does not form its anterior margin (Figure 7F). Though this feature is not found in any other *Emydops* specimens and is unique to ISIR 208, more specimens with this feature need to be discovered before it can be considered as a reliable specific character. Apart from this, ISIR 208 bears overall similarity with *E. platyceps* and is placed within *Emydops platyceps*.

Subfamily Cistecephalinae Broom, 1903

Genus **Cistecephalus** Owen, 1859

*Type species.*—*Cistecephalus microrhinus* Owen, 1876 (subsequent designation by King, 1988).

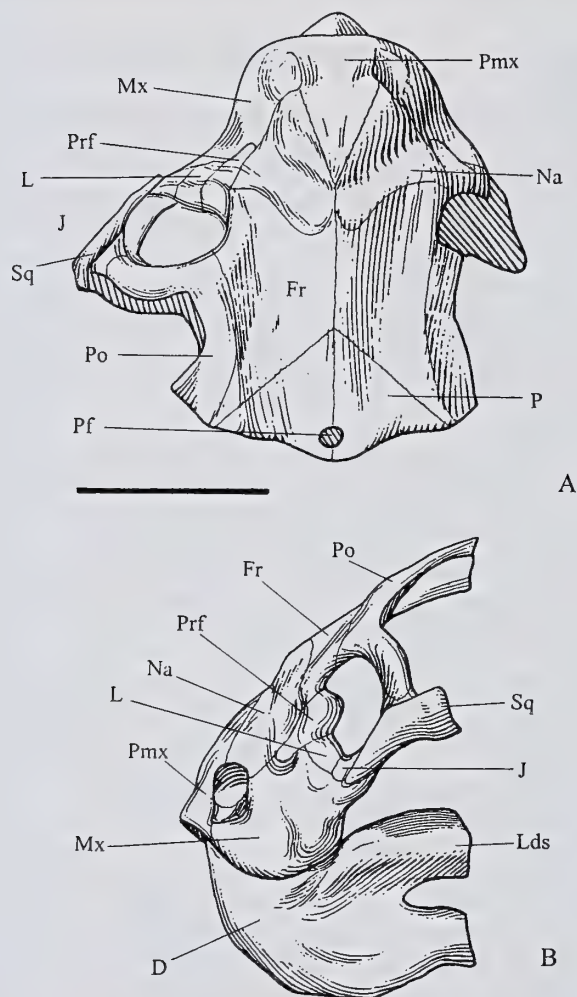
***Cistecephalus microrhinus* Owen, 1876**

Figures 2I–J, 8–10, 11A–B

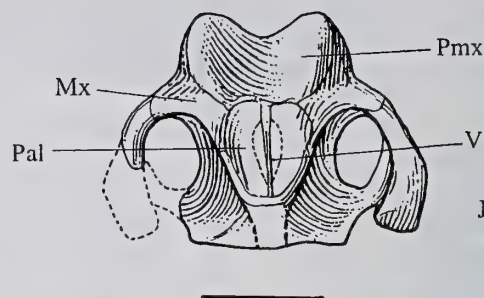
*Cistecephalus microrhinus* Owen, 1876, p. 63, pl. 64, fig. 4–7; King, 1988, p. 118, fig. 33 (see for prior synonymies).

*Holotype.*—BMNH R 47066, an imperfect skull from Stylkraans, Graaff-Reinet, Cape Province, South Africa; *Cistecephalus* Assemblage Zone, Late Permian.

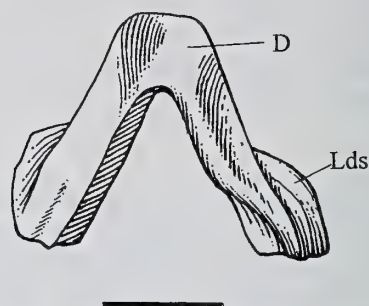
*Diagnosis.*—Small, toothless emydopids with broad or narrow intertemporal region; lacrimal foramen, postfrontal and preparietal absent; pterygoid meeting below parabasisphenoid complex; interpterygoidal vacuity absent; stapes perforated or deeply incised; prominent lateral



**Figure 8.** *Cistecephalus microrhinus* Owen, 1876. ISIR 210. Partial skull with lower jaw in **A**, dorsal and **B**, lateral views. Scale bar represents 20 mm.



**Figure 9.** *Cistecephalus microrhinus* Owen, 1876. ISIR 366. Anterior part of skull in ventral view. Scale bar represents 10 mm.



**Figure 10.** *Cistecephalus microrhinus* Owen, 1876. ISIR 367. Anterior part of lower jaw in dorsal view. Scale bar represents 10 mm.

dentary shelf (Keyser, 1973; King, 1988).

*Material.*—ISIR 210, anterior portion of a skull with attached lower jaw, lacking the posterior part of the zygomatic arch, squamosals, occiput and postdentary bones, ISIR 365, a laterally compressed skull with attached lower jaw, ISIR 366, left portion of skull, ISIR 367, snout region, ISIR 368, anterior part of a lower jaw.

*Repository.*—The specimens are housed in the Geology Museum, Indian Statistical Institute, Calcutta.

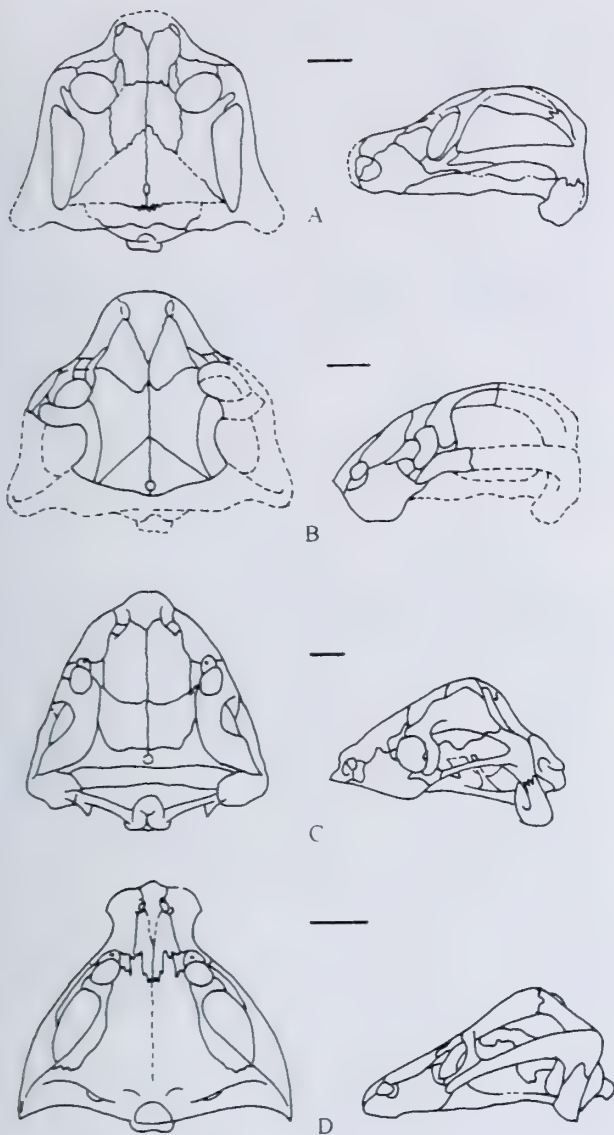
*Locality and horizon.*—The specimens were collected near Golet (Figure 1), Adilabad district, Andhra Pradesh, India from the Late Permian Kundaram Formation, Gondwana Supergroup.

*Description.*—

**Skull**

ISIR 210 is a small, triangular skull with a slight lateral and anteroposterior distortion. Its length along the dorsal midline from the anterior end of the premaxilla to the posterior end of the pineal foramen is 41 mm while the total length is inferred to be about 52 mm. Different measurements of ISIR 210 are given in Table 4. Its snout is short, broad and tapers anteriorly with the nostrils situated close to the midline and separated by a large, swollen and wedge-shaped premaxilla. The maxilla occupies the anterolateral sides of the skull. The septomaxilla is completely recessed within the nostril. The orbits are circular, relatively small, anterodorsally placed and separated by a wide interorbital





**Figure 11.** Skulls in dorsal and lateral views; **A–B**, *Cistecephalus microrhinus*. **A**, after Broili and Schroder, 1935; **B**, ISIR 210; **C**, *Cistecephaloides boonstrai* (after Cluver, 1974a); **D**, *Kawingasaurus fossilis* (after Cox, 1972). Scale bars represent 10 mm.

region. This region consists of large, paired nasals anteriorly and frontals posteriorly. The anterior part of the circumorbital rim is formed by the large, elongated prefrontal and rectangular lacrimal. The postfrontal is absent. The intertemporal region widens considerably (31 mm approx.) especially at the posterior end of the skull. A small, circular pineal foramen is situated at the far end of the skull roof. The paired parietals constituting the intertemporal bar are broad, widely exposed and laterally bordered by the slightly raised but narrow postorbital. The postorbital is separated from the prefrontal by the frontal. The preparietal is absent.

**Table 4.** Measurements of the skull (ISIR 210) of *Cistecephalus microrhinus*. Asterisk (\*) indicates inferred measurements. All measured in mm.

Parameters	<i>Cistecephalus microrhinus</i> (ISIR 210)
Skull length	52*
Preorbital snout length	17.5
Postorbital snout length	23
Length from anterior edge of premaxilla to posterior edge of pineal foramen.	41
Diameter of the pineal foramen	2
Interorbital width	28.5
Intertemporal width	31
Snout width	27.5

Beyond the pineal foramen, the posterior part of the skull and the zygomatic arches are broken.

In ISIR 210, the slender jugal is completely overlapped by the squamosal; the latter reaches the maxilla because of antero-posterior compression. The usual *Cistecephalus* feature of maxilla and squamosal separated by the jugal is preserved in ISIR 365. The palate of the specimen ISIR 210 cannot be studied as the lower jaw is in position and attached to the skull. The anterior part of the palate is studied from the specimens ISIR 365 and ISIR 367. It is edentulous and consists of a sharp palatal rim formed anteriorly by the premaxilla and posterolaterally by the maxilla. The palatines are very small and curved posteriorly. A narrow vomerine septum separates the very small internal nostrils.

#### Lower jaw

The lower jaw is described from the specimens ISIR 210, ISIR 365 and ISIR 368. It is short, robust and deep. The dentaries are completely fused at the symphysis and form sharp, transverse cutting edge anteriorly. Posterior to the cutting edge, the dorsal surface of the dentary is slightly raised and further posteriorly it bears a pair of ridges. Posteriorly the lower jaw is flared out laterally. Above the Meckelian fenestra is present a distinct lateral dentary shelf. The posterior ends of the specimens and the postdentary bones are not preserved in the specimens ISIR 210 and ISIR 367. In ISIR 210, the lower jaw is attached to the palate showing that the latter is much wider than the symphyseal region of the lower jaw.

**Discussion.** — The subfamily Cistecephalinae contains small, toothless emydopids with very broad intertemporal region lacking the postfrontal and preparietal (King, 1988). Other characteristic features of this subfamily include perforated or deeply incised stapes, vestigial or no interpterygoid vacuity, reduced palatine, premaxilla extended far back posteriorly, anterior edge of the dentary symphysis forming a sharp cutting edge and a prominent lateral dentary shelf.

This subfamily is composed of three genera, *Cistecephalus* Owen, 1876 (Figures 11A–B), *Cistecephaloides* Cluver, 1974a (Figure 11C) and *Kawingasaurus* Cox, 1972 (Figure 11D). The cranial and postcranial morphology

**Table 5.** Distinguishing features of *Cistecephalus*, *Cistecephaloides* and *Kawingasaurus* (sources: Broili and Schroder, 1935; Cox, 1972; Cluver, 1974a; King, 1988).

Parameters	<i>Cistecephalus</i>	<i>Cistecephaloides</i>	<i>Kawingasaurus</i>
Snout	Short and broad	Short and broad	Flattened, laterally expanded
Orbits	Large, anterolaterally placed orbits	Small	Small
Interorbital region	May be broad or narrow	Broad	Broad
Lacrimal foramen	Absent or present low down within the orbit	Large	Large
Relation between prefrontal, frontal and postorbital	Prefrontal separated from postorbital by frontal	Prefrontal meeting postorbital	Prefrontal separated from post-orbital by frontal
Postorbital	Relatively slender	Very robust	Relatively slender
Pineal foramen	Circular, situated at the far end of the intertemporal bar	Very small, insignificant	Absent
Squamosal	May be separated from maxilla by jugal	Separated from maxilla by jugal	Reaches maxilla
Otic region	Normal	Normal	Highly inflated

of these taxa have been studied in detail (Seeley, 1894; Broom, 1932, 1948; Broili and Schroder, 1935; Keyser, 1973 and Cluver, 1974a, b, 1978) and show that the features like the broad, triangular skull with wide interorbital and intertemporal regions, rounded occiput and absence of the interpterygoidal vacuity are of a highly specialised animal with fossorial habits. However, *Cistecephaloides* differ from *Cistecephalus* in having a very high skull roof, sloping anteriorly and with the prefrontal in sutural contact with a robust postorbital, while *Kawingasaurus* is distinguished by the absence of the pineal foramen and an inflated otic region. The other distinctive features of *Cistecephalus* are given in Table 5.

The Indian specimens exhibit a short snout, circular orbit, absence of the postfrontal, preoparietal and the lacrimal foramen, frontal separating the postorbital and prefrontal, wide intertemporal region, circular pineal foramen, transverse cutting edge of the dentary and prominent lateral dentary shelf (Figure 11B). These features clearly indicate that the specimens belong to the genus *Cistecephalus*.

A large number of *Cistecephalus* species were originally erected, distinguished by parameters such as their size differences, broad or narrow skull, and variations in the arrangement of the skull roof bones (Owen, 1876; Broom, 1932, 1948). All the fossils were collected from the Permian part of the Beaufort Group of South Africa. Keyser (1973) suggested that *Cistecephalus* species are members of a growth series and synonymised all the species with *C. microrhinus*, the latter being the only valid species of the genus. The Indian *Cistecephalus* is compared with the South African forms (SAM-PK-K6814, SAM-PK-K7667, SAM-PK-K7852, SAM-PK-K8304 and SAM-PK-10665) collected from the Late Permian part of the Beaufort Group of the Karoo Supergroup and housed in the South African Museum, Cape Town (Table 6). The total skull lengths of the African specimens studied vary between 42 mm and 63 mm. The skull length of ISIR 210 and ISIR 365 (Table 6) falls well within that range. The interorbital width of the African specimens varies between 10 and 18 mm and that of

**Table 6.** Comparative measurements of several specimens of *Cistecephalus*. All measured in mm. Index to the abbreviations is given in Table 3.

Specimen	Parameters				
	SL	SW	IO	IT	IT/IO
SAM-PK-K6814	54.38	59.06	16.88	39.38	2.33
SAM-PK-K7667	63	70	17	25	1.47
SAM-PK-K7852	42	37	10	25	2.5
SAM-PK-10665	48.46	42.69	11.54	32.31	2.8
SAM-PK-K8304	55	62	18	45	2.5
ISIR 210	52*	—	28.5	31	1.1
ISIR 365	46.4	—	18.2	23	1.2

\*inferred

ISIR 365 is 18.2 mm. The specimen ISIR 210 shows a marked increase in interorbital width (about 28 mm) because of antero-posterior compression. However, in all other aspects, the Indian specimens bear an overall similarity with the African forms.

### Concluding remarks

The Permian in India is very poorly represented by vertebrate fossils. Apart from some palaeoniscoid fishes and temnospondyl amphibians from other Gondwana basins (Werneburg and Schneider, 1996), the Kundaram vertebrates record the sole occurrence of the Permian amniotes in India. Studies have shown that the fauna is largely represented by the two species of *Endothiodon* (Ray, 2000). The present work further strengthens this fauna with the addition of three more genera, *Pristerodon* (*P. mackayi*), *Emydops* (*E. platyceps*) and *Cistecephalus* (*C. microrhinus*). King (1992) reported the presence of *Oudenodon*. The only non-dicynodont member is a captorhinid (Kutty, 1972). Although the study of the Kundaram fauna is far from completion, it is worthwhile to mention some important aspects



of the fauna.

1. The most complete vertebrate record of the Late Permian period is found in the lower part of the highly fossiliferous Beaufort Group of the Karoo Supergroup, South Africa and is subdivided into six biozones. The Kundaram fauna bears a remarkably close similarity to that of the Beaufort Group of South Africa. *Pristerodon* has a wide range covering all the five Permian biozones of the Beaufort Group except for the *Eodicynodon* Assemblage Zone (Rubidge, 1995), and hence is not useful for precise correlation. *Endothiodon* first appears in the *Pristerognathus* Assemblage Zone but predominates in the *Tropidostoma* Assemblage Zone. In this latter zone, *Cistecephalus* occurs very infrequently and *Emydops* makes its first appearance (Figure 12). In contrast, *Endothiodon* persists as a rare fossil while *Cistecephalus* becomes abundant in the succeeding *Cistecephalus* Assemblage Zone. This zone also records the first appearance of *Oudenodon*.

However, the Kundaram fauna shows a preponderance of *Endothiodon* amounting to about thirty individuals with four or five partial skulls of *Cistecephalus* and *Emydops*. The dominance of *Endothiodon* followed by *Emydops* and *Cistecephalus* in the Kundaram fauna indicates a broad correlation with the *Tropidostoma* and *Cistecephalus* Assemblage Zones of the Beaufort Group of South Africa. The Kundaram Formation is also correlated with the basal beds of the Madumabisa Mudstones of Zambia, the Ruhuhu and lower part of the Kawinga Formation of Tanzania and the Morro Pelado Member of the Rio do Rasto Formation of Brazil. It suggests a Late Permian Tatarian age for the Kundaram Formation.

2. Another distinctive feature of the Kundaram vertebrate fauna is the small size of its individual members. *Endothiodon* shows two distinct clusters of skull size. *E. mahalanobisi* has an average SL of about 160 mm and is much smaller than the other known *Endothiodon* species, while that of *E. uniseries* is about 350 mm. Other dicynodonts of the Kundaram Formation like *Pristerodon*

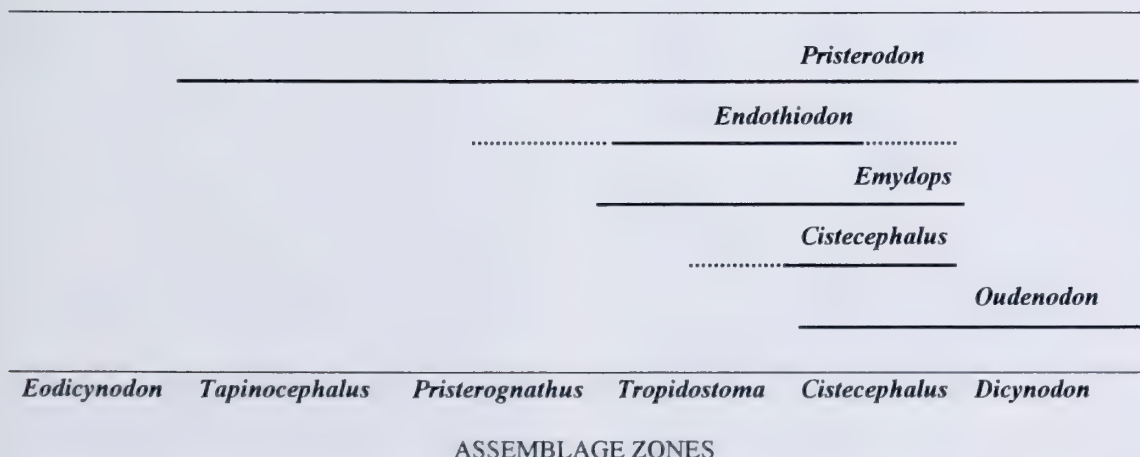
*mackayi* (SL ca. 50.6 mm), *Emydops* sp. (SL ca. 47.8) and *Cistecephalus microrhinus* (SL ca. 50 mm) are also small. This smallness of size is also reflected in the captorhinid (SL ca. 50 mm).

The dominance of the small forms in the Kundaram fauna is comparable with that of the *Cistecephalus* Assemblage Zone. In this zone, more than 70% of the total faunal assemblage is composed of small forms, in marked contrast to that of the underlying *Tropidostoma* Assemblage Zone. The latter zone is characterised mainly by medium to large dicynodonts such as *Rhachiocephalus* (Rubidge, 1995). There are too many unknown parameters, to say with confidence what might have caused this size differentiation. It may be due to preservational bias, transportational sorting or palaeoclimatic and palaeogeographic influences and necessitates further study of the Permian Kundaram fauna.

3. The distribution of Kundaram dicynodonts, *Endothiodon*, *Oudenodon*, *Pristerodon*, *Emydops* and *Cistecephalus*, in the now widely separated geographic areas (Table 7) suggests that there was no apparent physical barrier between these regions. Moreover, the Pangean distribution of these dicynodont-bearing regions shows a broad and regular zone, extending from Brazil in the west to India in the east (Ray, 1999). It indicates the close proximity of the continents during that time and a lack of endemism or provinciality among these genera.

**Table 7.** Distribution of the five dicynodont genera (after Anderson and Cruikshank, 1978; King, 1992; Ray, 1999).

South Africa	India	Mala- gasy	Tan- zania	Zambia	Mozam- bique	Brazil
<i>Pristerodon</i>	+		+	+		
<i>Endothiodon</i>	+		+	+	+	+
<i>Emydops</i>	+			+		
<i>Cistecephalus</i>	+					
<i>Oudenodon</i>	+	+		+		



**Figure 12.** Ranges of the Kundaram dicynodont genera present in the Beaufort Group, Karoo Supergroup, South Africa (after Rubidge, 1995).

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## Appendix

### Institutional abbreviations

AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; ISI, Indian Statistical Institute, Calcutta; SAM, South African Museum, Cape Town.

### Anatomical abbreviations

Alv	Alveolus	Pal	Palatine
Ang	Angular	Pf	Pineal foramen
Ar	Articular	Pmx	Premaxilla
Bo	Basioccipital	Po	Postorbital
Bs	Basisphenoid	Pof	Postfrontal
D	Dentary	Pp	Preparietal
Eo	Exoccipital	Pr	Prootic
Fr	Frontal	Prf	Prefrontal
Fm	Foramen magnum	Pt	Pterygoid
Ip	Interparietal	Ptf	Post-temporal fenestra
Ipt.v	Interpterygoidal vacuity	Q	Quadrate
J	Jugal	Qj	Quadratojugal
Jf	Jugular foramen	Rl	Reflected lamina
L	Lacrima	Sph	Sphenethmoid complex
Lds	Lateral dentary shelf	St	Stapes
Lf	Lacrima foramen	Smx	Septomaxilla
Mx	Maxilla	So	Supraoccipital
Mf	Meckelian fenestra	Sp	Splenial
Na	Nasal	Sq	Squamosal
Op	Opisthotic	V	Vomer
P	Parietal		





# Quantification of optically granular texture of benthic foraminiferal walls

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**Abstract.** Three main textures may occur in optically granular walls of hyaline calcareous foraminifera: mosaic granular, jagged granular, and minute granular. The size and shape of the optical granules within them indicates that these wall textures are intimately related to the crystalline arrangement of the units and their elements, and also to the wall thicknesses of the foraminiferal tests. Highly complex minute-granular textures are observed if the foraminiferal tests are large and walls are thick. In general, crystallographically compound and intermediate wall structures correspond to the minute-granular texture. Both formsize (ratio of perimeter to area) and Shannon-Wiener index for polarized crystal units explain these different wall textures well. This study suggests a method for quantification of wall textures based on image processing.

**Key words:** benthic foraminifera, crystal unit, ecology, optical textures, test walls

## Introduction

Hyaline calcareous walls of benthic foraminiferal tests consist of small crystallites and their assembled crystal units. Hansen (1968, 1970) clarified these crystalline structures by scanning electron microscope studies, and in the 1970s several authors examined these foraminiferal test structures in diverse foraminiferal taxa (e.g., Banner and Williams, 1973; Stapleton, 1973; Bellefleur, 1974a, b; Conger *et al.*, 1977). Features of the crystalline structures in test walls are revealed by high interference colors under polarizing microscopy. Wood (1949) introduced the terms radial and granular structures for these optical features of foraminiferal walls. Nomura (1983, 1988) further recognized variations in each optical texture, and subdivided granular structure into mosaic, jagged, and minute (Figure 1.1–1.3), and radial textures into distinct and indistinct. These subdivisions of the granular walls are based on the optical grain size and the structure. Although a clear-cut distinction between them is sometimes difficult, the mosaic granular has larger and less jagged appearances than the jagged one. Optical grains of the minute granular are conspicuously small and complicated in comparison with the mosaic and jagged ones. These optical textures clearly reflect the complexity of crystalline structures consisting of various optical axes of the crystal units and their elements (Nomura, 1983).

The optical textures of foraminiferal walls have mainly been utilized for systematic purposes. Loeblich and Tappan (1964, 1974, 1987) used optical features of

foraminiferal walls for their hierarchical classification. This classification now needs to be reexamined in view of increased knowledge. Apart from its application to foraminiferal systematics, wall texture can be used to assist in interpretation of foraminiferal ecology and paleoecology (Nomura, 1988, 1997). In a preliminary report (Nomura, 1997), I suggested that granular textures show variations corresponding to the preferred ecology of individual species. The best example is found in the ecological difference between epifaunal and infaunal species. Mosaic granular texture is mainly found in infaunal taxa, and minute granular texture is seen in epifaunal taxa (Nomura, 1997). It is empirically understood that the crystal units of foraminiferal tests show variations in their perimeter and area in polarized light. As there are gradual changes among the mosaic, jagged, and minute granular textures, however, application of these optical textures to ecology and paleoecology is not definitive. Information on the ecological and ontogenetic characters of the wall textures is still limited.

In order to clarify the optical grains of these textures by quantitative analyses, I examined live and dead specimens having different textures and different growth stages. Observations of the wall texture using a polarizing microscope are particularly useful on account of the simple methodology employed. Definition of analytical methods is needed however to perform reliable comparisons of foraminiferal wall textures.



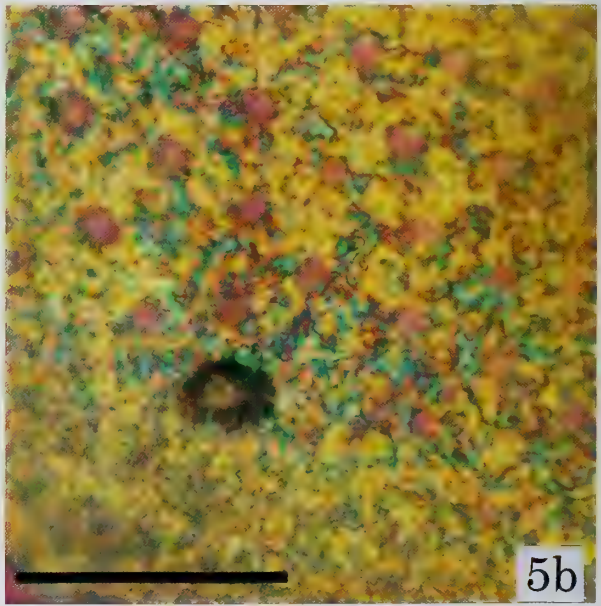
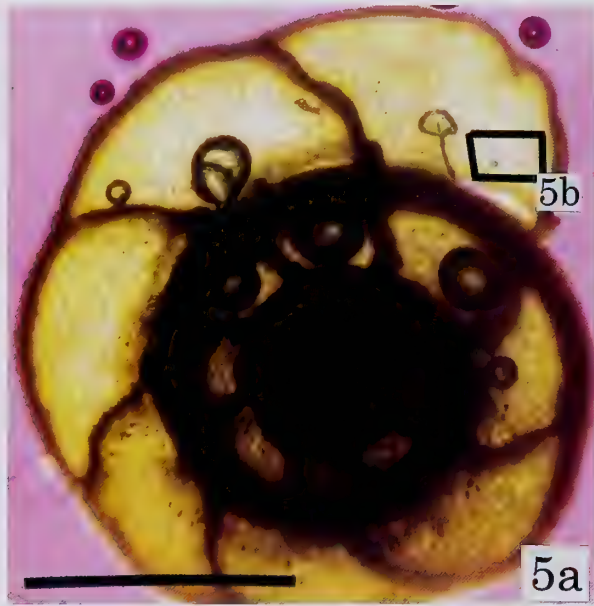
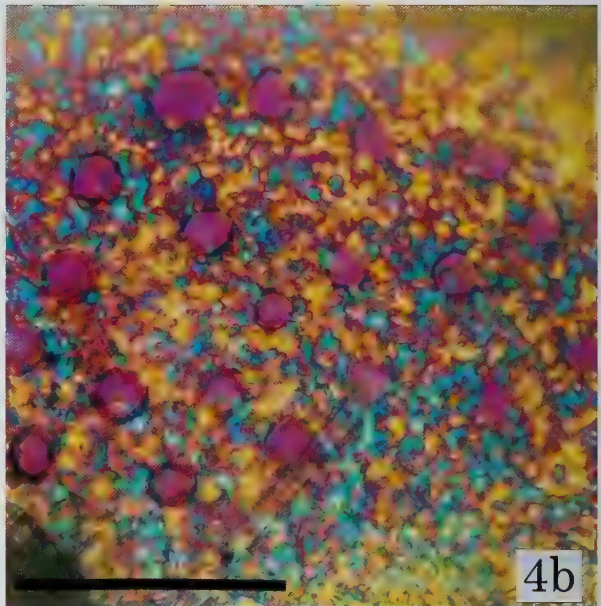
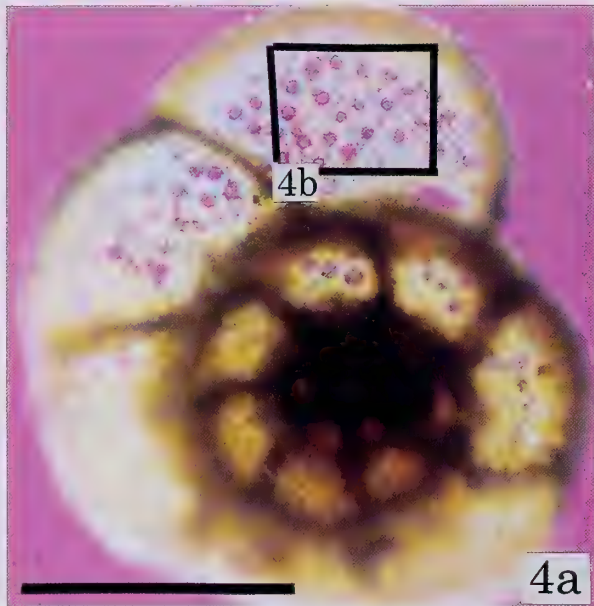
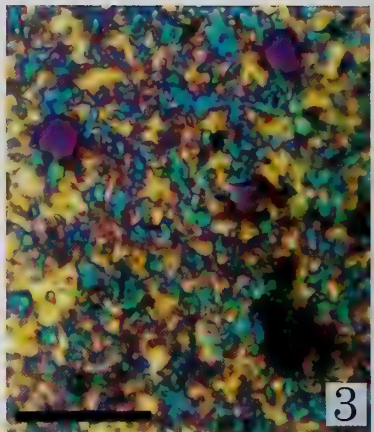
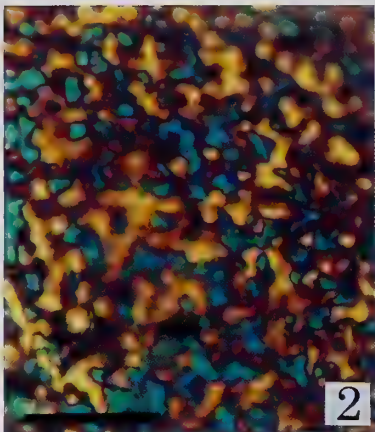
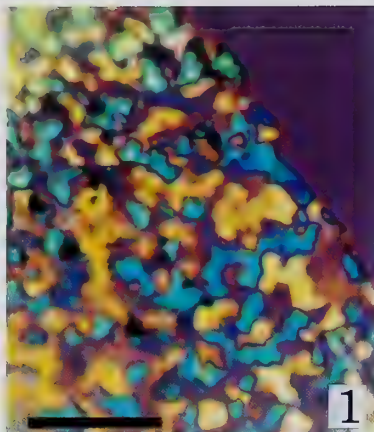




Table 1. Species examined in this study.

taxa	test size (mm)	wall thickness ( $\mu\text{m}$ )	depth in m (sample)	condition
<i>Anomalinoidea glabratus</i> (Cushman)	0.24–0.56	2.5–15.0	54(HK-1')	dead
<i>Cassidulina reniforme</i> (Norvang)	0.14–0.20	1.0–2.5	194(HN3-9')	dead
<i>Chilostomella oolina</i> Schwager	0.38–0.49	1.0–3.8	Pliocene Ilioka Formation, Choshi **	fossil
<i>Cibicides lobatulus</i> (Walker and Jacob)	0.38–0.78	6.8–18.2	54(HK-1')	dead
<i>Cibicides refulgens</i> Montfort	0.22–0.71	4.5–12.5	54(HK-1')	dead
<i>Cibicoides pseudoungerianus</i> (Cushman)	0.56–0.83	8.0–11.3	99(HK-4')	dead
<i>Cibicoides wuellerstorfi</i> (Schwager)	0.23–0.72	1.5–20.0	99(HK-4')	dead
<i>Elphidium advenum</i> (Cushman)	0.20–0.62	2.0–12.5	54(HK-1')	live, dead
<i>Fursenkoina pauciloculata</i> (Brady)	0.29–0.83	1.3–6.2	54(HK-1')	live, dead
<i>Globocassidulina oriangularata</i> Belford	0.17–0.33	2.0–5.0	99(HK-4')	dead
<i>Gyroidina orbicularis</i> d'Orbigny	0.20–0.49	2.5–14.0	99(HK-4')	dead
<i>Gyroidinoides nipponicus</i> (Ishizaki)	0.22–0.37	3.8–4.0	54(HK-1')	dead
<i>Heterolepa subhaidingeri</i> (Parr)	0.40–0.86	6.3–19.5	99(HK-4')	live
<i>Nonionellina labradorica</i> (Dawson)	0.22–0.39	1.0–4.7	150(CB4-1')	live
<i>Nonion manpukuziensis</i> Otuka	0.27–0.66	2.5–7.5	54(HK-1')	dead
<i>Oridorsalis umbonatus</i> (Reuss)	0.18–0.46	1.0–4.3	150(CB4-1')	dead
<i>Pullenia bulloides</i> d'Orbigny	0.16–0.32	2.8–5.0	150(CB4-1')	dead
<i>Paracassidulina neocarinata</i> (Thalmann)	0.206–0.32	2.2–5.5	99(HK-4')	dead

\* KT-90-15, Tansei-maru Cruise, off Shimane and Yamaguchi Prefectures, Sea of Japan (Ocean Research Institute, Univ. of Tokyo)

\*\* Well preserved

## Methods

The last chambers of live and well preserved dead specimens of 18 foraminiferal species were analyzed (Table 1). Foraminiferal tests were first embedded in glycerin jelly and covered with a thin glass cover slip as in standard preparation for microscope observation. Tests were crushed and fragments of the final chamber walls were arranged carefully by pressing the glass under a binocular microscope while the jelly was liquid enough to allow the wall pieces to move.

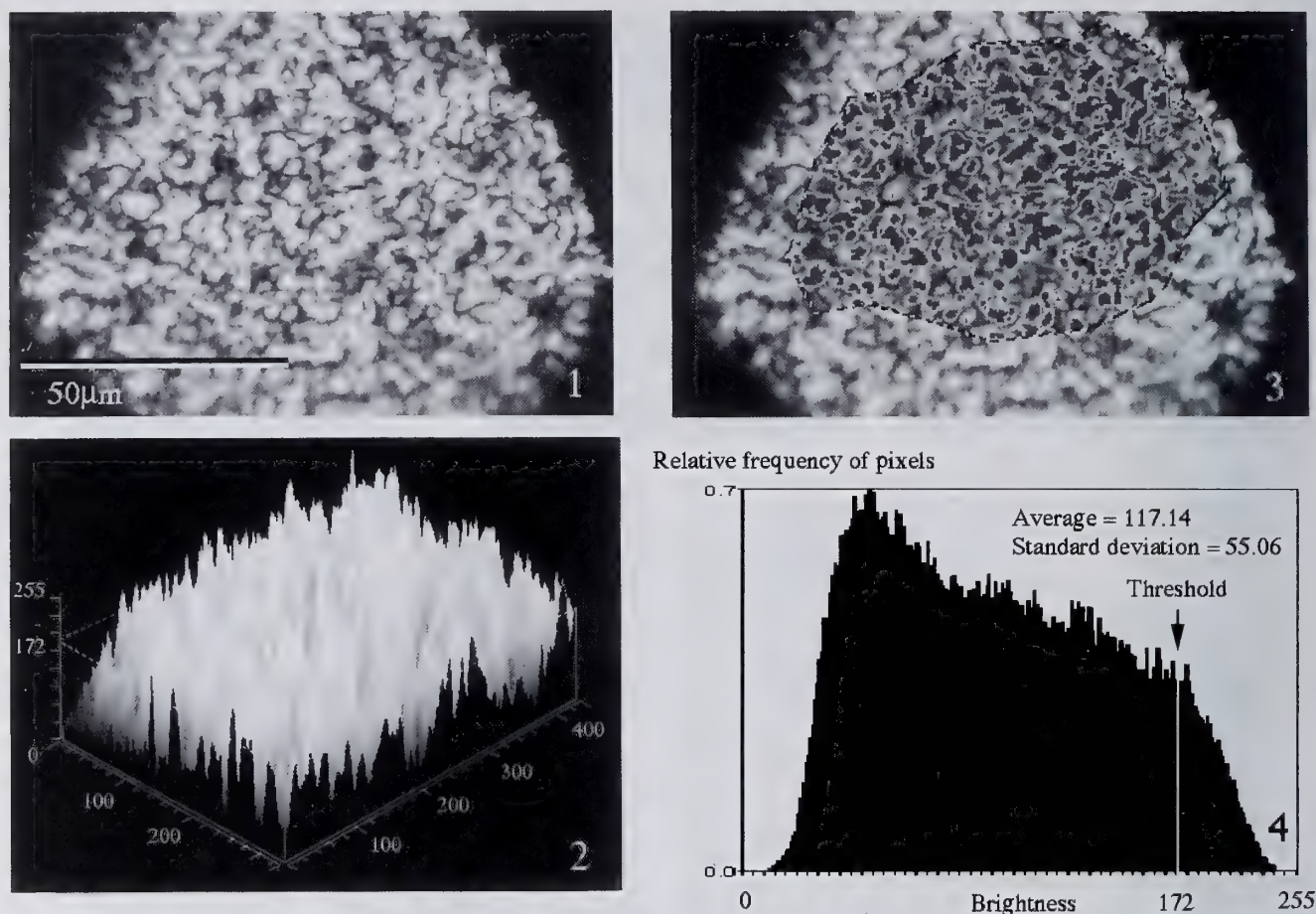
Observations and measurements of the crystal units were carried out under a polarizing microscope at a magnification of  $\times 400$ . Measurements of the wall thickness were made on final wall fragments set vertically on the glass at the magnification of  $\times 1000$ , after wall texture photography. Crystal units were observed most effectively using the first-order interference colors arising from insertion of a gypsum plate. The image analysis was carried out using Winroof (version 3.5.2; Mitani Corporation, 2000), which runs on Windows computers. The observations were made at an angle of  $45^\circ$  to the optically positive or negative orientations of the crystal units. Two methods were used to quantify the texture image. Firstly the perimeters and areas of manually selected crystal units were measured to calculate the ratio of perimeter to area (A/P ratio or formsize) (Nomura, 1997). Ten to twenty crystal units were measured for each wall

piece. Because this method is subjective, sometimes selection errors can be made, especially when the unit is not clearly differentiated from neighboring units. To avoid such selection errors, I applied a second method that detects crystal units after color processing which disintegrates the original color image into RGB (red, green, and blue).

Crystal units are more effectively distinguished in the G (green) image at specific threshold values (Figure 2). Thresholding is a brightness discrimination, which selects pixels belonging to features of interest (Russ, 1990). Possible values range from 0 to 255. A block model of the green image, in which the peaks correspond to the brightness intensities, is shown in Figure 2.2. Selection of the crystal unit areas is thus critically controlled by the threshold values. Various threshold values were examined to find the best texture images. Statistically, pixel brightness has a characteristic frequency distribution for each texture, and usually shows a normal distribution (Figure 2.4). The following formula was used to determine the threshold value for each specimen examined: Threshold value = Average threshold value + Standard deviation. Between 100 and 500 areas of selected crystal units were counted for each specimen.

The selected unit images were subsequently converted to binary images (Figure 2.3) and their areas, perimeters, and formsizes then calculated. These measurements were

← **Figure 1.** Variations of optically granular wall texture. **1.** Mosaic-granular texture of *Chilostomella ovoidea*. Scale bar = 50  $\mu\text{m}$ . **2.** Jagged-granular texture of *Elphidium advenum*. Scale bar = 50  $\mu\text{m}$ . **3.** Minute-granular texture of *Cibicoides pseudoungerianus*. Scale bar = 50  $\mu\text{m}$ . **4a, 4b.** Horizontal section of a small *Heterolepa subhaidingeri* and close-up of the final chamber wall showing the minute-granular texture. Scale bar: 4a, 200  $\mu\text{m}$ , 4b, 100  $\mu\text{m}$ . **5a, b.** Horizontal section of a larger *H. subhaidingeri* and close-up of the final chamber wall showing indistinct crystal unit boundaries. Scale bar: 5a, 500  $\mu\text{m}$ , 5b, 100  $\mu\text{m}$ .



**Figure 2.** Explanations for the image processing of *Fursenkoina pauciloculata*. **1.** Green image of the texture separated from the blue and red images. **2.** Block diagram of the green image. Thresholding is the brightness value used to distinguish particular images from others, ranging from 0 to 255. Dotted horizontal lines indicate the threshold value (172) in this analysis. **3.** Binary image of the crystal unit areas at threshold value 172. **4.** Histogram showing the relative frequency of pixel brightness (0–255). The averaged brightness is 117.14 and the standard deviation is 55.06. Thresholding at 172 (sum of the average and the standard deviation) accounts for 20.35% of the selected texture.

based on the binary images at threshold values of 130–240. The formsize of each crystal unit is calculated by the formula:  $\text{Formsize} = 2 \cdot (\text{Area}) / (\text{Perimeter})$ . Values are  $\geq 1$ . If the formsize is 1, the crystal unit is perfectly circular and its radius is 1. The A/P ratio (Nomura, 1997) is a simple expression of this formsize.

The areas of the selected crystal units show a wide variation between 1 to 2000s pixels. Statistical values with high standard deviation make the comparison of the formsize unreliable. However, both the number of the selected areas and the number of pixels they contain represent the difference between the textures, so that they conform to the concept of ecological heterogeneity that accounts for the amount of order or disorder in any given part of the wall. The Shannon-Wiener information function ( $H'$ ) is herein applied to evaluate the diversity of the textures:

$$H' = -\sum_{i=1}^N (P_i) (\log_2 P_i)$$

where  $N$  is the total number of the crystal units selected and  $P_i$  is the proportion in the  $i$ th-selected area to the total areas selected. Higher values of  $H'$  indicate the textures are characterized by a more complex crystalline arrangement, whereas lower values represent textures consisting of more simple arrangements.

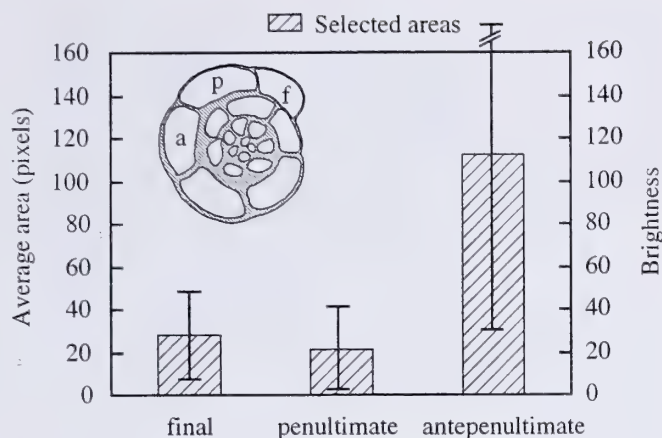
It is difficult to measure the thicknesses of fixed parts of the walls, because breakage occurs randomly during crushing. Analysis was limited to flat pieces of final chamber walls. Sutural areas consist of complicated crystalline structures showing interwoven crystal units and elements. Such areas are not suitable for this analysis. Wall thickness is proportional to test size, and so increases in individuals with growth, even though it varies between foraminiferal species. Thus, careful selection of wall fragments is necessary if reliable results are to be obtained.



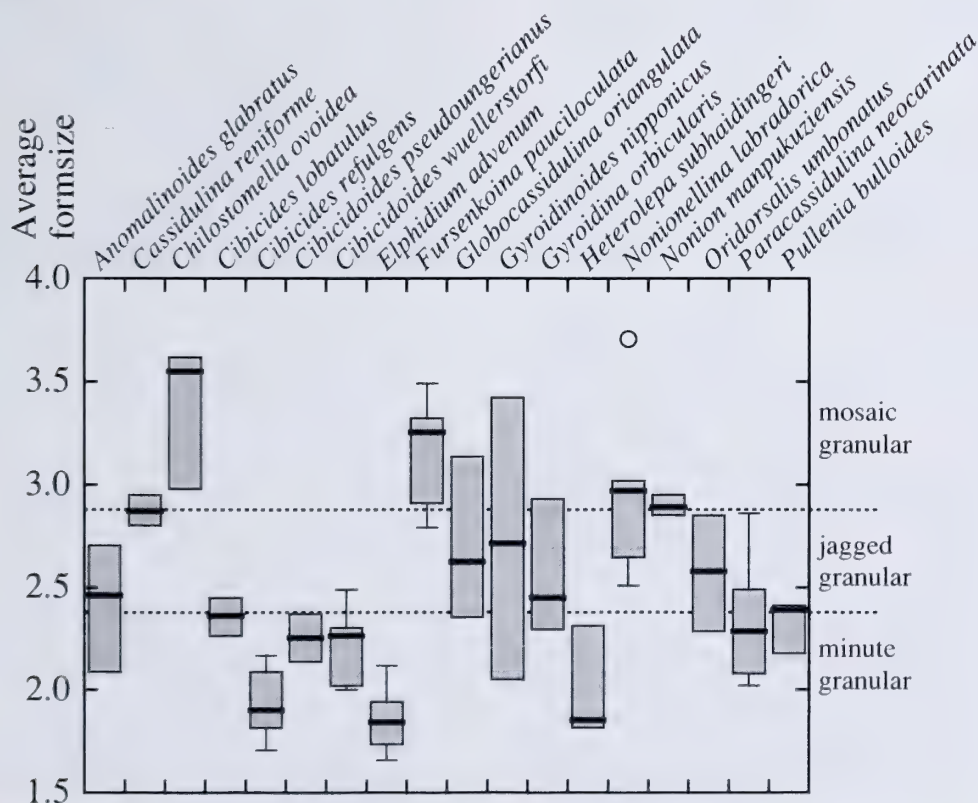
## Results

The smaller specimens examined here (maximum diameter 0.15–0.25 mm) usually have final chamber walls between 1.0–5.0  $\mu\text{m}$  thick. However, mature specimens of species such as *Chilostomella ovoidea*, *Nonionellina labradorica*, and *Cassidulina reniforme* may also have thin walls (< 5.0  $\mu\text{m}$ ). Large specimens (0.4–0.9 mm diameter) of species such as *Heterolepa subhaidingeri* show a wide range of wall thickness (6.3–19.5  $\mu\text{m}$ ; Table 1). Wall thickness differs between taxa, and appears to be reflected in wall texture. Thin-walled specimens show well defined boundaries between crystal units displaying distinct blue, red, and yellow areas, but thicker specimens have indistinct boundaries, and blue and red areas are much reduced. These color changes are caused by the interference order of polarizing light, because internal refraction of incident light occurs in every crystal element in the unit and at the unit boundary. Thin-walled crystal units present first-order interference color, but thicker walls containing assembled crystal units produce multiple interference. Brightness of pale yellow images thus increases with increasing wall thickness.

Change of optical texture in relation to the wall thickness can also be seen within individuals as they grow. As observed in *Cibicidoides pseudoungerianus* tests of differing



**Figure 3.** Results of averaged areas with standard deviations for the last three chambers of a sectioned *Oridorsalis umbonatus*. Threshold value is 130. Increased areas in the antepenultimate chamber are caused by indistinct boundaries between the crystal units. f: final chamber. p: penultimate. a: antepenultimate.



**Figure 4.** Average form size in each species. Many species have a wide variation in form size, which is related to the different textures. Mosaic-granular texture is typified by form size of > 2.8; form size of minute-granular textures are < 2.4; and values for jagged-granular texture lie between 2.4 and 2.8. Hatched boxes enclose 50% of the form sizes and the tops and bottoms of the box mark  $\pm 25\%$ . Thick horizontal line indicates the median. Small circle is an exceptional value.

size (Figure 1.4, 1.5), unit boundaries of crystal units in the final chamber wall can be easily distinguished. In thicker walls, higher interference makes the boundaries less clear (Figure 1.5b). As noted above, the yellowish color in the antepenultimate chamber is caused by higher-order interference colors. The variations in average areas of the selected crystal units and the brightness in the walls of the last three chambers of *Oridorsalis umbonatus* are shown in Figure 3. The average area of the crystal units in the antepenultimate chamber walls is four to five times larger than that in the walls of the final and the penultimate chambers. Areal increase in the antepenultimate chamber walls is clearly related to the brightness, which makes the unit boundary indistinct. Clear discrimination of the crystal units is possible in the final chamber, where wall thickness is usually  $< 3\text{--}4\text{ }\mu\text{m}$ .

Based on the form size, mosaic-granular texture occurs in *Chilostomella ovoidea* and many immature specimens (i.e., small specimens) of *Cassidulina reniforme*, *Fursenkoina pauciloculata*, *Globocassidulina orianguata*, *Gyroidinoides nipponicus*, *Gyroidina orbicularis*, *Nonion manpukuziensis* and *Nonionellina labradorica*. This texture is recognized by form sizes of over 2.8 (Figure 4). The walls of *Nonionellina labradorica* show atypical mosaic-granular texture, where either the optically positive or negative conditions are dominant in the apertural face. Optical axes of the crystal elements are equally arranged over large areas, but are oblique to the test surface. This texture can also be seen in taxa having larger apertural faces, such as *Nonion* and *Nonionella*. Typical minute-granular texture is shown by most species of the genera *Cibicidoides*, *Cibicides*, and *Heterolepa*. This texture reflects the original complexity of their crystalline arrangement. In the Cibicidinae (Bellemo, 1974b, 1976), this is termed compound and the intermediate structure. Similar form size is also seen in other mature specimens of *Anomalinoides glabratus*, *E. advenum*, *G. orianguata*, *G. nipponicus*, *G. orbicularis*, *O. umbonatus*, *Paracassidulina neocarinata* and *P. bulloides*, except for *Chilostomella ovoidea* and *Cassidulina reniforme*. However, their crystalline structures differ slightly from those of the Cibicidinae in having larger crystal units and herringbone structure (e.g., Nomura, 1983). Thus, the minute-granular texture is formed by the original complex crystalline structure and by an apparent feature of thick walls consisting of mosaic and jagged-granular textures. The boundary between minute-granular and jagged-granular may be around a form size of 2.4 (Figure 4). Jagged-granular texture is usually recognized between 2.4 and 2.8.

These three wall textures show wide variations in the measured form size values. In particular, thinner walls ( $< 5\text{ }\mu\text{m}$ ) are characterized by high standard deviation values (Figure 5). Gradual changes between the different textures also occur. Excepting the Cibicidinae, most species show three differing textures according to the growth stages of the individual: mosaic-granular texture corresponds to the stage of new chamber formation or the younger growth stage of individual foraminifera; jagged- and minute-granular textures correspond to the full-grown stages of individuals.

A significant relationship is indicated between modified form size (form size divided by the square root of the number

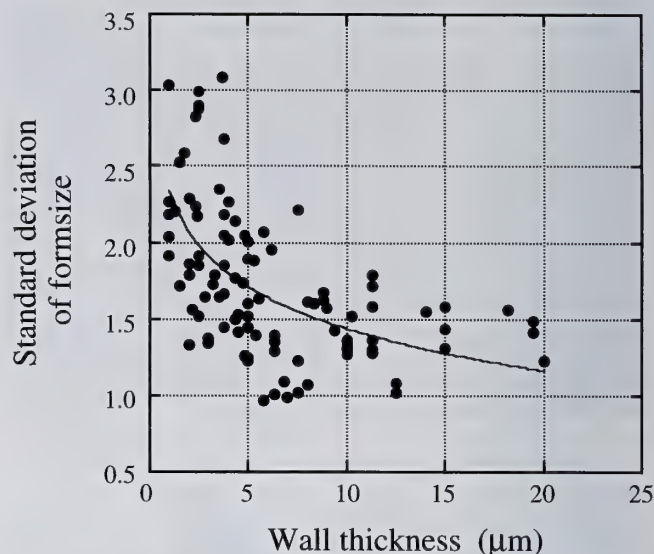


Figure 5. Plots of standard deviation of form size and wall thickness showing large variations in thinner test walls.

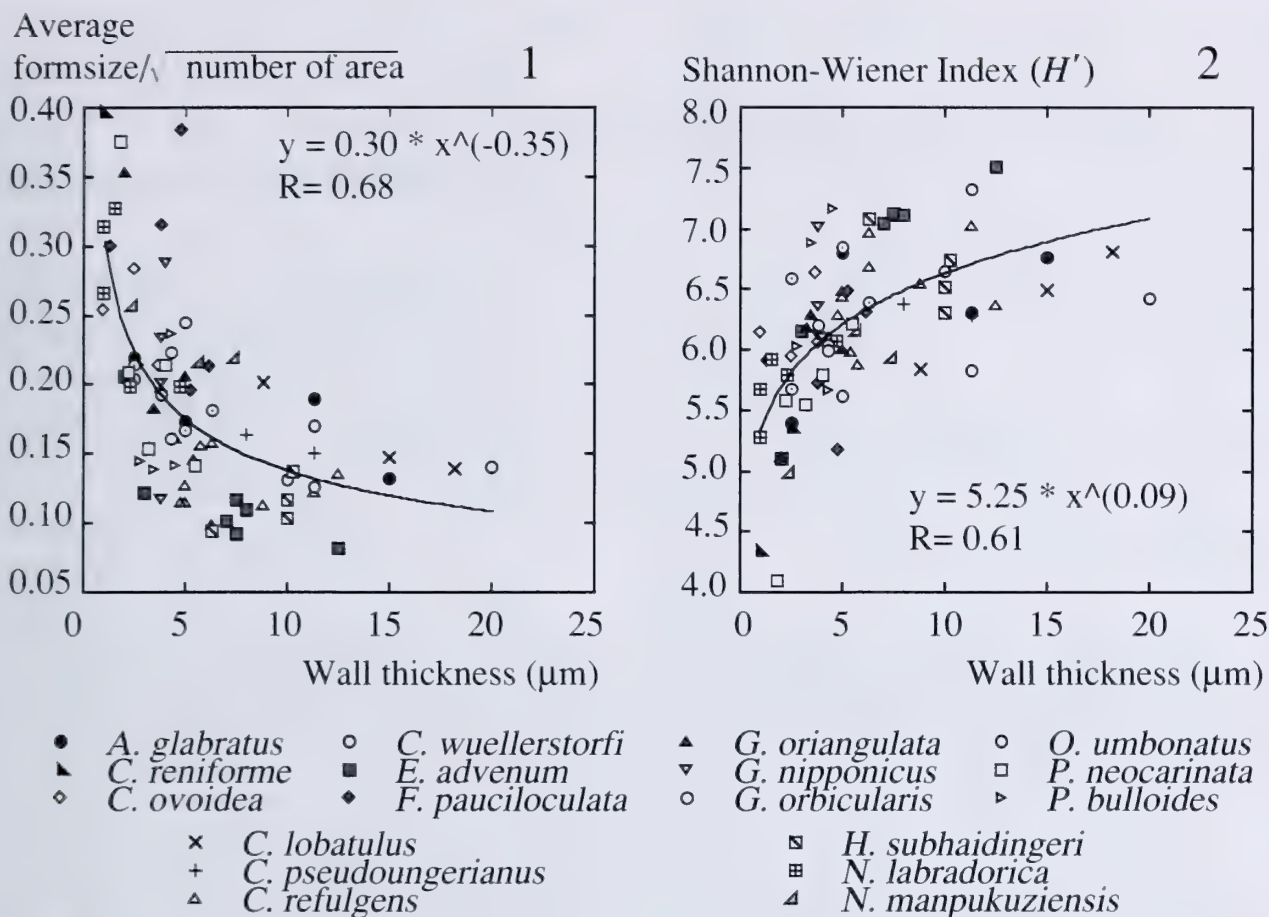
of selected crystal units) and wall thickness (Figure 6.1). This relationship can be expressed as an exponential, with  $r = 0.68$ . The form size is divided by the square root of the number of crystal units because form size is dependent on the number of selected areas. Mosaic granular textures are characterized by low numbers of selected crystal units and higher form sizes, whereas minute-granular textures have larger numbers of crystal units and lower form size values. The results clearly indicate that larger form sizes have thinner walls, whereas specimens with smaller form size values have thicker walls and/or originally smaller and complex crystal units. Shannon-Wiener information theory is the other quantitative expression to account for the heterogeneity of selected units that consist of large and small areas. The result of this information function is opposite to the relationship between form size and wall thickness (Figure 6.2). It is thus negatively correlated with modified form size at a statistically significant level ( $p < 0.001$ ) (Figure 7). If the Shannon-Wiener information index is higher, then the modified form size is smaller, and textures are complex. Conversely, if the information index is lower, then modified form size is higher and textures are simpler.

As a result, distribution of respective wall textures on the form size overlaps among different species, due to changes in the wall texture through growth. Little change in the wall texture is observed between the final and the preceding walls, as well as among different-sized specimens of thinly walled species such as *Chilostomella ovoidea* and *Cassidulina reniforme*. These species are characterized by having larger original crystal units and additional thin laminae in walls formed subsequently.

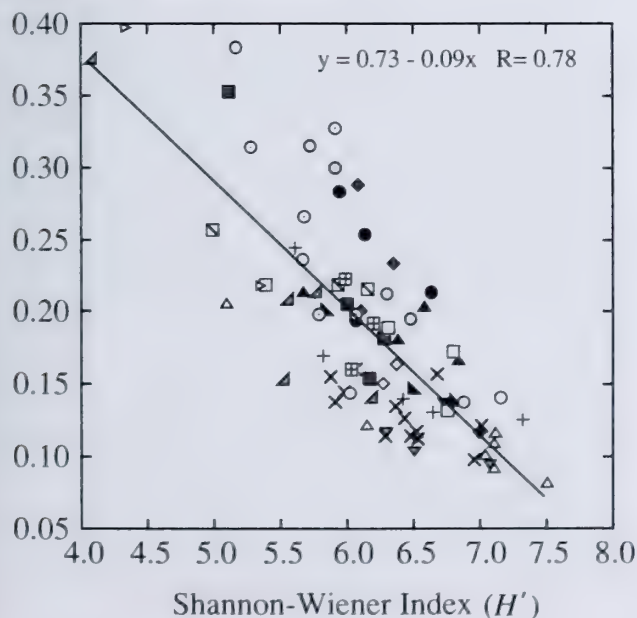
## Discussion and Conclusions

Mosaic, jagged and minute granular optical wall textures result from the arrangement of crystal units and the ele-





Average  
form size /  $\sqrt{\text{number of area}}$



ments within any wall thickness. Mosaic-granular texture is formed by larger crystal units and thinner walls, and was once named "clumpy crystalline structure" (Nomura, 1983). Jagged-granular texture is correlated with "intricate crystalline structure" (Nomura, 1983). Minute-granular texture is formed by two types of crystalline structures: 1) intricate crystalline structures within thicker walls, and 2) complex arrangement of crystal elements such as the compound and intermediate structures of Bellemo (1974b, 1976). Ratios of the perimeter to the area of the selected crystal unit have been introduced as a method of quantitatively discriminating these wall textures (Nomura, 1997). However, initially this method used manual selection of crystal units and thereby sometimes produced errors. Criteria for the selection of crystal units are needed. The present study confirms that the intimate relationships between optical texture and crys-

talline structure can be recognized in walls showing first-order interference colors. Even in this case, image processing is required to overcome individual variations. Several adjoining crystal units may apparently form large single units in polarizing light. Such units must be eliminated to make realistic measurements and comparisons. The thresholding proposed is a simple method of discriminating various texture images.

Classification of optically granular texture in hyaline calcareous foraminifera (Nomura, 1988, 1997) is not only a species character, but is also related to the wall thickness of the foraminiferal test and the complexity of crystalline structures. In general, thinner walls show mosaic-granular texture, whereas thicker walls and complex crystalline structures (compound and intermediate) exhibit minute-granular texture. Jagged-granular texture is present in walls of intermediate and moderate thickness. To evaluate these optical textures, the relationships between form sizes of the crystal units were examined for differing growth stages of foraminiferal individuals of selected species. The results suggest that the form size of the crystal units shows a gradual change in accordance with the crystalline complexity of the test walls in different foraminiferal growth stages. The relationship between form size and the wall thickness is statistically significant and exponential. Shannon-Wiener information theory is applicable for quantification of the textures, and the Shannon-Wiener index is negatively correlated with the modified form size parameter.

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# Origin of the Ceratitida (Ammonoidea) inferred from the early internal shell features

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**Abstract.** The early internal shell features in 40 species of the Goniatitida, Prolecanitida and Ceratitida are described on the basis of well-preserved specimens from the Carboniferous and the Permian of North America, England, Siberia and Urals. Seven morphotypes were recognized in the species examined by differences of the caecum shape (bottle-shaped, gourd-shaped, subelliptical, or elliptical), the proseptum length on the dorsal side (long or short), position of the second septum (close to proseptum or not) and initial position of the siphuncle (ventral, subcentral, or central). *Paracelmites elegans*, the oldest known representative of the Ceratitida, has a long proseptum on the dorsal side, a relatively small ammonitella angle, the second septum does not appear in close vicinity to proseptum, and the siphuncle is ventral. These features are essentially the same as those of the prolecanitid *Daraelites elegans*. This fact supports the hypothesis that the Ceratitida evolved from the Prolecanitida, probably *Daraelites*.

**Key words:** Ceratitida, early internal shell features, Goniatitida, phylogeny, Prolecanitida

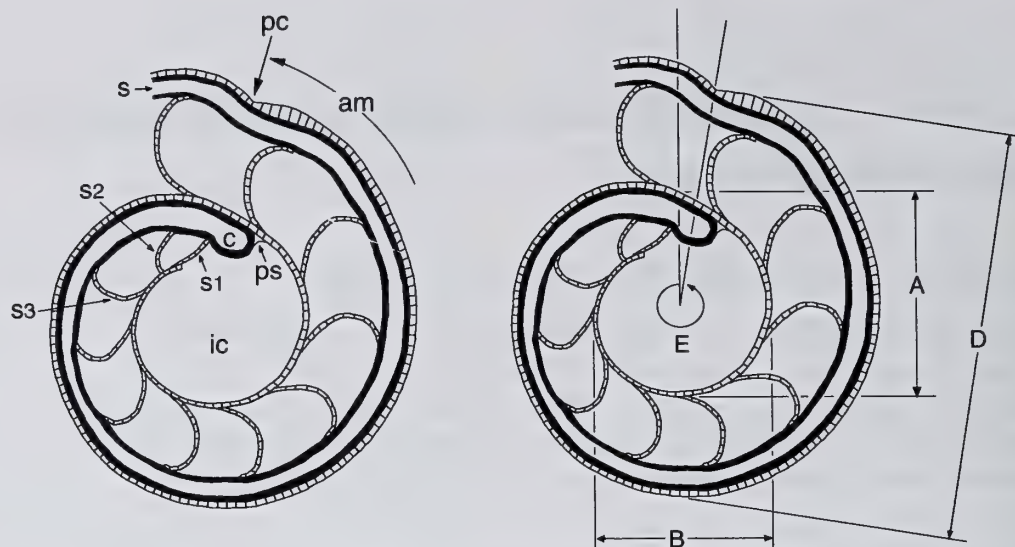
## Introduction

The Ceratitida, which is the dominant ammonoid order of the early Mesozoic and one of the major orders of Ammonoidea, ranged from early Permian to the end of Triassic times, and has an almost worldwide distribution (Hewitt *et al.*, 1993; Page, 1996). The origin of this order has been thought to be from a member of the Prolecanitida, because previous authors believed that both taxa shared a common lobe development (i.e., VU type of Ruzhencev, 1960, 1962 or U type of Schindewolf, 1934, 1953; see Smith, 1932; Spath, 1934; Spinosa *et al.*, 1975; Shevyrev and Ermakova, 1979; Saunders and Work, 1997). Zakharov (1983, 1984, 1988), however, showed that the Prolecanitida (Medlicottida in Zakharov, 1983) and the Permian Ceratitida (Paraceltitina in Zakharov, 1984) do indeed share the same lobe developmental type, (i.e., VLU type of Ruzhencev, 1960, 1962 or A type of Schindewolf, 1934, 1953), but one identical to that of the Goniatitida. He also pointed out the difficulty in determining the ancestor of the Ceratitida based on the lobe development patterns, because all early to middle Permian ammonoids have the

same lobe development pattern (Zakharov, 1984). After his works, no detailed observations of various shell characters have been done as a basis for discussion of the ancestor of the Ceratitida.

Since Branco (1879, 1880), the ammonoid early internal shell features have been studied by many authors, and it has been determined that there are a number of common characters in the early shells of all ammonoids. States of these characters appear to be stable at suborder or superfamily levels (Druschits and Khiami, 1970; Druschits and Doguzhaeva, 1974, 1981; Tanabe *et al.*, 1979; Tanabe and Ohtsuka, 1985; Ohtsuka, 1986; Landman *et al.*, 1996). This fact suggests that the early internal shell features are strongly constrained phylogenetically, and therefore, it is possible to investigate the higher phylogenetic relationships within the Ammonoidea by analyzing these character state changes (Shigeta, 1989).

As compared with Jurassic and Cretaceous ammonoids, Carboniferous and Permian ammonoids have been little studied for their early internal shell features. Most previous studies (Shul'ga-Nesterenko, 1926; Böhmers, 1936; Miller and Unklesbay, 1943; Bogoslovskaya, 1959; Zakharov,



**Figure 1.** Diagrams of the internal shell structure (left) and measurements (right) of the early ammonoid shell in median section. The terminology is from Branco (1879, 1880), Grandjean (1910), and Drushchits and Khiami (1970). Abbreviations: am: ammonitella; c: caecum; ic: initial chamber; pc: primary constriction; ps: prosiphon; s: siphuncular tube; s1: proseptum (first septum); s2: primary septum (second septum); s3: third septum; A: maximum initial chamber size; B: minimum initial chamber size; D: ammonitella size; E: ammonitella angle.

1978) excluding Tanabe *et al.* (1994) and Landman *et al.* (1999) are based on optical microscopic observations. Detailed microstructural relationships of the morphologic features have received little examination.

We have studied the early internal shell features of some Carboniferous and Permian ammonoids belonging to the Goniatitida, Prolecanitida and Ceratitida, by means of scanning electron microscopy. In this paper, we describe some of our observations and discuss the results of our analysis with special reference to the origin of the Ceratitida.

#### Material and methods

Five species of the Prolecanitida, 34 species of the Goniatitida and one species of the Ceratitida have been examined (Appendix 1). Specimens of these ammonoids were collected from the Carboniferous and Permian strata of South Urals (Kazakhstan), Siberia (Russia), England and the U.S. mid-continent (Nevada and Texas). They include genera and species studied and figured by Tanabe *et al.* (1994). Higher categories of these genera and species were determined following the classification of Bogoslovskaya *et al.* (1999).

Every specimen was cut and polished along the median plane. The polished surface was etched with 5% acetic acid for a few minutes; the etched surface was washed with distilled water, dried in air, and then coated with gold or platinum using an ioncoater. The early internal features of each specimen were observed by means of a JEOL model JSM-5310 scanning electron microscope. Four characters: maximum initial chamber size, minimum initial chamber size, ammonitella size and ammonitella angle (= spiral length of ammonitella in degrees), were measured on the etched sur-

face using a digital micrometer (accuracy  $\pm 0.001$  mm) attached to a Nikon model V16D profile projector.








Figure 1 illustrates the terms used to describe the morphologic features of the early shell in median section. The terminology is based on Branco (1879, 1880), Grandjean (1910), and Drushchits and Khiami (1970) (see Landman *et al.*, 1996, figure 1). The specimens observed are deposited at the University Museum, University of Tokyo (UMUT) for those described by Tanabe *et al.* (1994) and at the National Science Museum, Tokyo (NSM) for the remaining specimens.

#### Observations

##### Prolecanitida and Goniatitida

The early whorls of the Carboniferous and Permian Prolecanitida and Goniatitida consist of initial chamber (protoconch), caecum, prosiphon, proseptum (first septum), septa, siphuncle, septal neck and outer shell wall, as in other Paleozoic and Mesozoic Ammonoidea. The maximum initial chamber size in median section (A in Figure 1) ranges from 0.356 mm to 0.645 mm in the Prolecanitida and from 0.356 mm to 0.590 mm in the Goniatitida (Appendix 2). The ammonitella diameter (D in Figure 1) ranges from 0.702 mm to 1.250 mm in the Prolecanitida and from 0.660 mm to 1.048 mm in the Goniatitida (Appendix 1). The ammonitella angle (E in Figure 1) is generally small ( $328\text{--}355^\circ$ ) in the Prolecanitida and relatively large ( $352\text{--}385^\circ$ ) in the Goniatitida. The early internal shell features of the species examined can be classified into seven morphotypes; here named for the genera that best show each variation: *Epicanites*, *Neopronorites*, *Daraelites*, *Goniatites*, *Maratho-*  
*nites*, *Agathiceras* and *Thalassoceras* morphotypes (Figure



Morphotype		Shape of caecum in median section	Length of prosepium (dorsal side)	Prosepium & 2nd septum (dorsal side)	Initial position of siphuncle
<i>Epicanites</i>		Bottle-shaped	Long	Separate (fairly)	Ventral
<i>Neopronorites</i>		Gourd-shaped	Long	Separate (a little)	Ventral
<i>Daraelites</i>		Bottle-shaped	Long	Separate (a little)	Ventral
<i>Goniatites</i>		Subelliptical	Long	Close	Ventral
<i>Marathonites</i>		Elliptical	Short	Close	Ventral
<i>Agathiceras</i>		Elliptical	Short	Close	Central
<i>Thalassoceras</i>		Elliptical	Short	Close	Subcentral

**Figure 2.** Comparison of the early internal shell features in seven morphotypes of the Carboniferous and Permian ammonoids. Each morphotype is named for the genera that best show each variation.

2). There is no intermediate form between a pair of these internal shell feature morphotypes in our data base. All of the morphotypes have a circular initial chamber in median section and a short prosiphon.

*Epicanites morphotype*.—In median section, caecum is elongate and subelliptical (bottle-shaped), without a conspicuous constricted base at prosepium and second septum; prosiphon is short and gently curved ventrally, and prosepium resting on dorsal side of initial chamber wall is long and strongly convex adapically. Second septum is convex adorally in median section, with a retrochoanitic septal neck, and is located far from prosepium. Siphuncle keeps ventral position throughout ontogeny.

*Akmilleria electaensis*, *Artioceras rhipaeum* (Figure 3.5, 6) and *Epicanites loeblichii* (Figure 4.1, 2) possess the early internal shell morphology of this morphotype. Early internal shell features of this morphotype have been reported in other Medlicottioidea (Shul'ga-Nesterenko, 1926; Böhmers, 1936; Miller and Unklesbay, 1943; Bogoslovskaya, 1959).

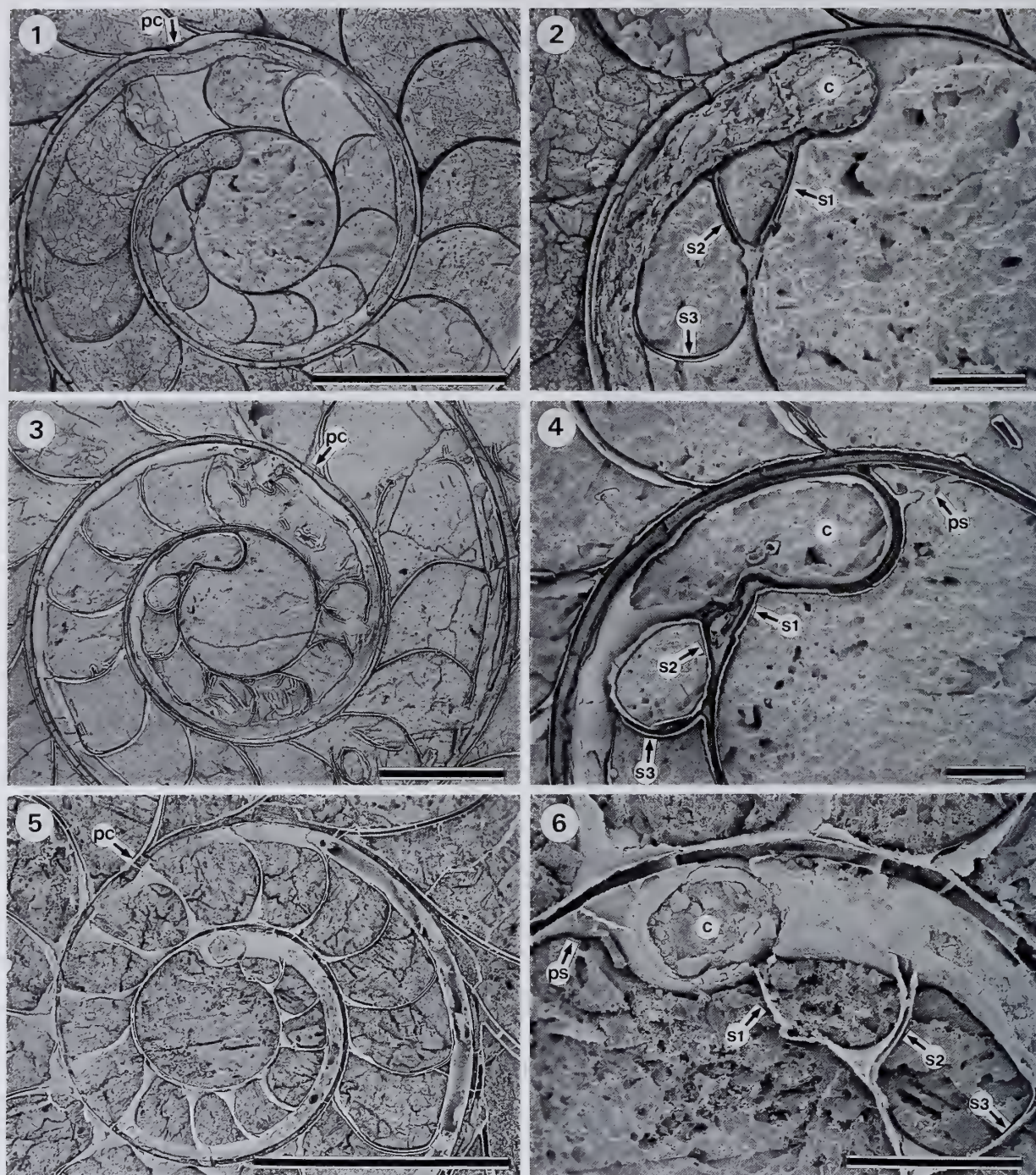
*Neopronorites morphotype*.—Caecum is gourd-shaped,

with a slightly constricted base at the prosepium, bulging part between prosepium and second septum, and gradual contracting part after second septum. Prosiphon is short, tube-like and straight. Prosepium resting on dorsal side of initial chamber wall is relatively long and slightly convex adorally in median section. Second septum is slightly concave adorally in median section, with a retrochoanitic septal neck, and is located relatively far from prosepium. Siphuncle is ventral throughout ontogeny.

*Neopronorites skvorzovi* (Figure 3.3, 4) possesses the early internal shell morphology of this morphotype, as described by Zakharov (1986). A similar shaped caecum was described in *Parapronorites cf. bififormis* by Shul'ga-Nesterenko (1926), hence she named it as a double caecum. Böhmers (1936), Miller and Unklesbay (1943) and Bogoslovskaya (1959) reported similar early internal shell features in other Pronoritoidea.

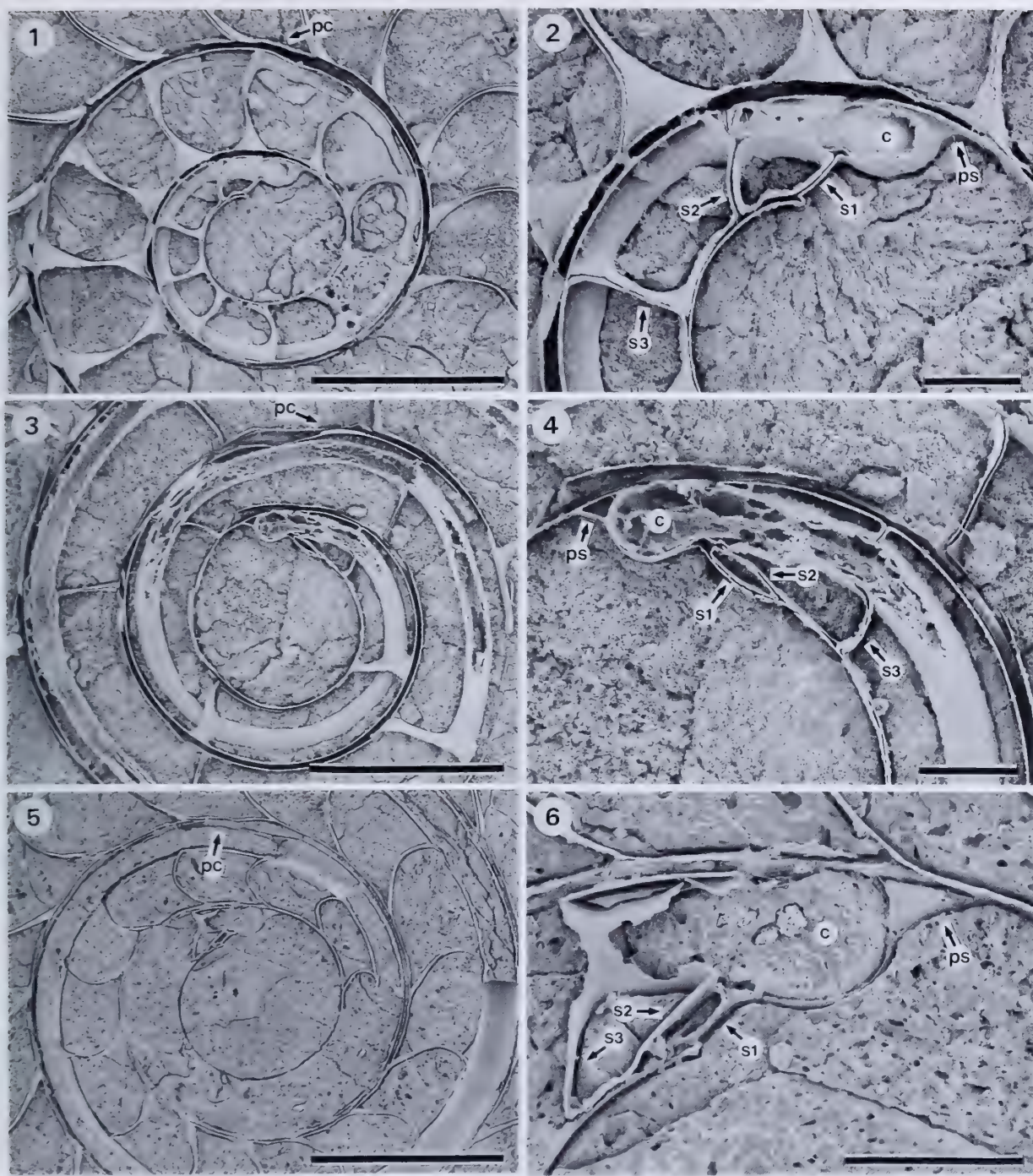
*Daraelites morphotype*.—Caecum is elongate and subelliptical (bottle-shaped), without a conspicuous constricted base at prosepium and second septum. Prosepium resting on





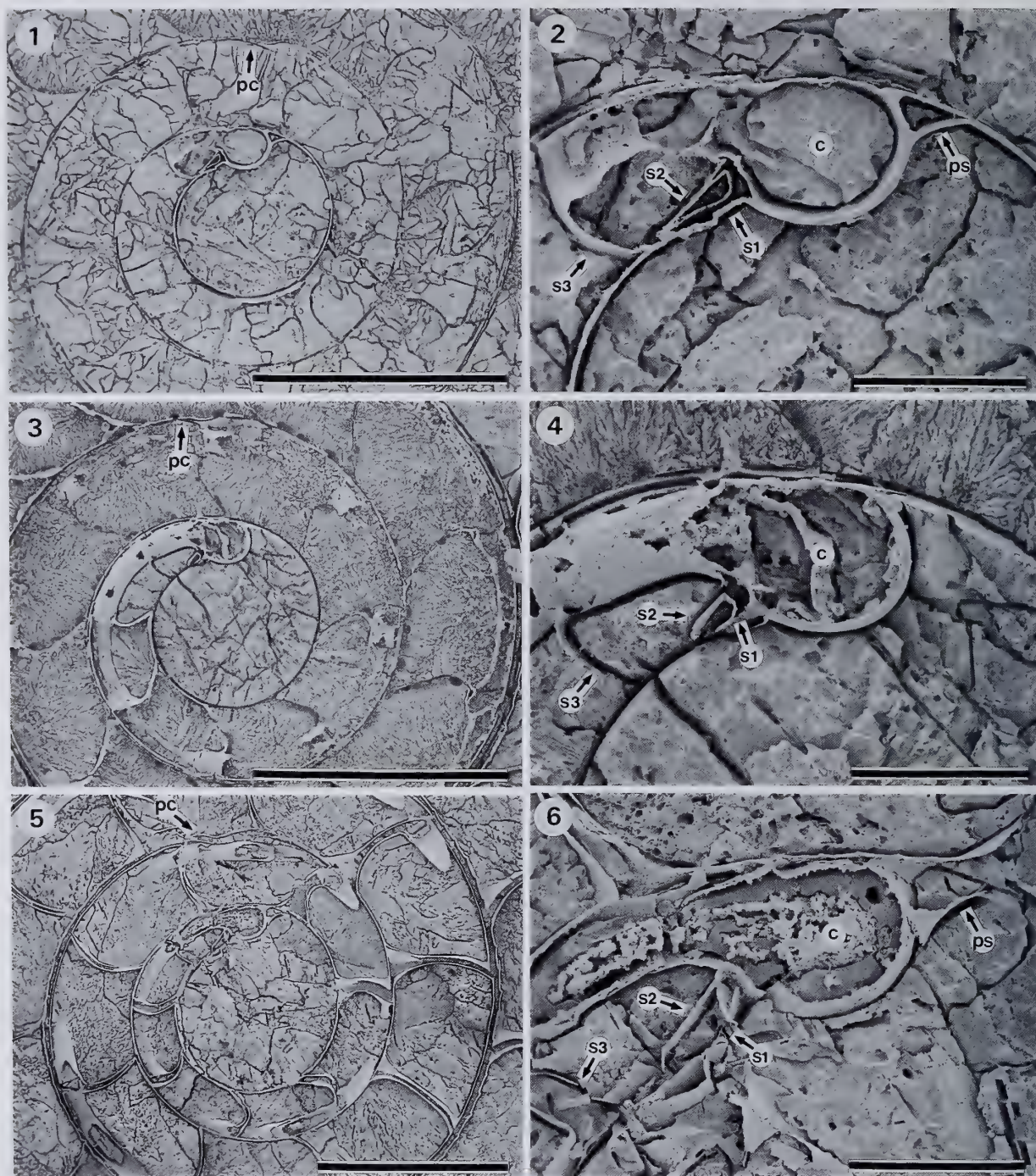
**Figure 3.** Median sections through the early whorls of the Permian prolecanitids. Over views of the early whorls showing the primary constriction (pc) (1, 3, 5) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4, 6). Scale bars in 1, 3 and 5: 0.5 mm. Scale bars in 2, 4 and 6: 0.1 mm. **1, 2.** *Daraelites elegans* Tchernow (Prolecanitoidea), Artinskian, South Urals (NSM PM16189). **3, 4.** *Neopronorites skvorzovi* (Tchernow) (Pronoritoidea), Artinskian, South Urals (NSM PM16190). **5, 6.** *Artioceras rhipaeum* (Ruzhencev) (Medlicottioidea), Artinskian, South Urals (NSM PM16192).





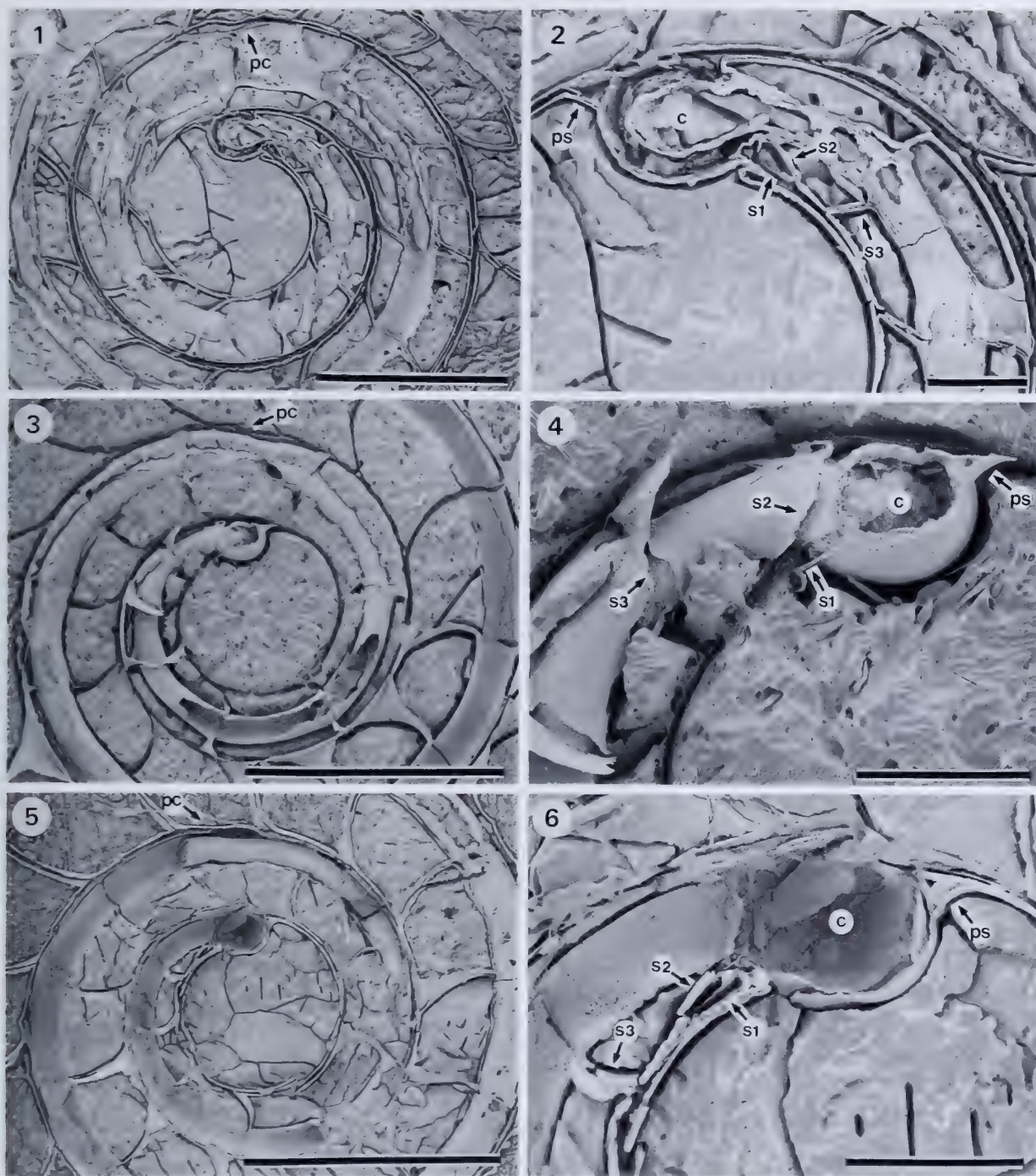
**Figure 4.** Median sections through the early whorls of the Carboniferous ammonoids. Overviews of the early whorls showing the primary constriction (pc) (1, 3, 5) and close-up of the prosiphon (ps), the caecum (c), the prosepium (s1), the second septum (s2) and third septum (s3) (2, 4, 6). Scale bars in 1, 3 and 5: 0.5 mm. Scale bars in 2, 4 and 6: 0.1 mm. 1, 2. *Epicanites loeblichii* Miller & Furnish (Prolecanitida: Prolecanitoidea), Chesterian, Oklahoma (NSM PM16188). 3, 4. *Girtyoceras meslerianum* (Girty) (Goniatitida: Dimorphoceratoidea), Chesterian, Oklahoma (NSM PM16193). 5, 6. *Cravenoceras incisum* (Hyatt) (Goniatitida, Neoglyphioceratoidea), Chesterian, Texas (NSM PM16198).





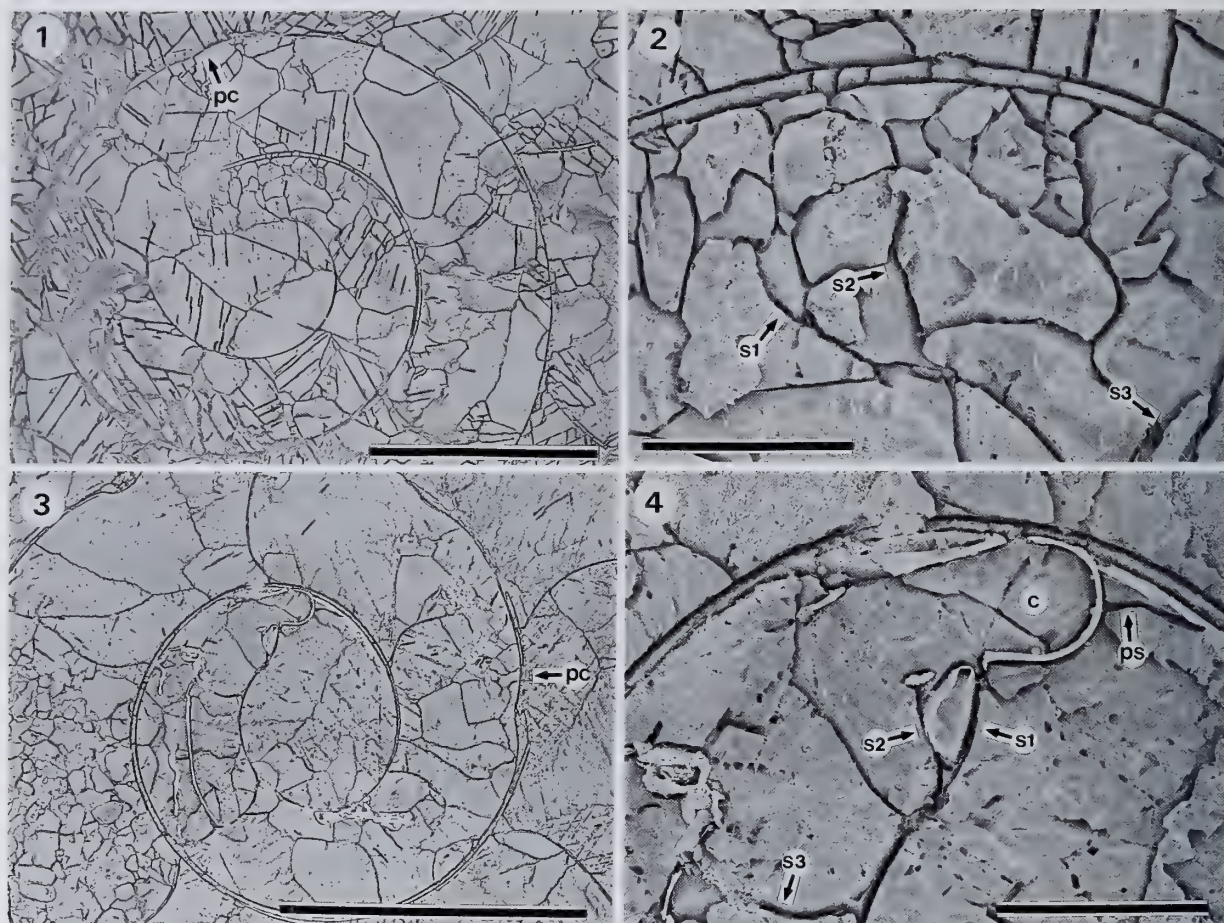
**Figure 5.** Median sections through the early whorls of the Permian goniatitids. Overviews of the early whorls showing the primary constriction (pc) (1, 3, 5) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4, 6). Scale bars in 1, 3 and 5: 0.5 mm. Scale bars in 2, 4 and 6: 0.1 mm. **1, 2.** *Popanoceras annae* Ruzhencev (Popanoceratoidea), Artinskian, South Urals (NSM PM16214). **3, 4.** *Marathonites invariabilis* (Ruzhencev) (Marathonitoidea), Artinskian, South Urals (NSM PM16207). **5, 6.** *Uraloceras* sp. (Neiococeratoidea), Wolfcampian, Nevada (NSM PM16213).





**Figure 6.** Median sections through the early whorls of the Permian goniatitids. Overviews of the early whorls showing the primary constriction (pc) (1, 3, 5) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4, 6). Scale bars in 1, 3 and 5: 0.5 mm. Scale bars in 2, 4 and 6: 0.1 mm. **1, 2.** *Agathiceras uralicum* (Karpinsky) (Goniatitoidea), Artinskian, South Urals (NSM PM16195). **3, 4.** *Thalassoceras gemmellaroi* Karpinsky (Thalassoceratoidea), Artinskian, South Urals (NSM PM16203). **5, 6.** *Crimites subkrotowi* Ruzhencev (Adrianitoidea), Artinskian, South Urals (NSM PM16204).





**Figure 7.** Median sections through the early whorls of the Permian and Triassic ceratitids. Overviews of the early whorls showing the primary constriction (pc) (1, 3) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4). Scale bars in 1 and 3: 0.5 mm. Scale bars in 2 and 4: 0.1 mm. 1, 2. *Paraceltites elegans* Girty (Xenodiscoidea), Roadian, Texas (NSM PM16215). 3, 4. *Nordopficeras jacksoni* (Hyatt & Smith) (Noritoidea), Spathian, Bear Lake area, Idaho (NSM PM16216).

dorsal side of initial chamber wall is long and slightly convex adapically in median section. Second septum is convex adorally in median section, with a retrochoanitic septal neck, and does not appear to be in close vicinity to proseptum. Siphuncle keeps a ventral position throughout ontogeny.

*Daraelites elegans* possesses the early internal shell morphology of this morphotype (Figure 3.1, 2). Early internal shell features of this morphotype have been found in other species of *Daraelites* (Böhmers, 1936; Miller and Unklesbay, 1943).

*Goniatites morphotype*.—In median section, caecum is subelliptical, without a conspicuous constricted base at proseptum and second septum; prosiphon is short and gently curved ventrally, and proseptum on dorsal side is long and slightly convex adapically. Second septum is attached to proseptum on the dorsal side, forming a necklike structure in median section. Siphuncle keeps a ventral position throughout ontogeny.

Genera in the major superfamilies of the Carboniferous Goniatitida, including those in the Dimorphoceratoidea, Goniatitoidea, Neoglyphioceratoidea, Somoholitoidea and Gastrioceratoidea listed in Appendix 1, possess the early internal shell morphology of this morphotype (Figure 4.3–6; Appendix 1). Our observations are consistent with the descriptions by previous authors (Böhmers, 1936; Miller and Unklesbay, 1943; Tanabe *et al.*, 1994).

*Marathonites morphotype*.—In median section, caecum is ellipsoid with a strongly constricted base at proseptum and second septum; prosiphon is short and gently curved ventrally, and proseptum on dorsal side is short and convex adapically. Second septum is attached to proseptum on dorsal side, forming a necklike structure in median section. Siphuncle keeps a ventral position throughout ontogeny.

Many superfamilies of the Permian Goniatitida, including the Adrianitoidea, Marathonitoidea, Neoicoceratoidea and Popanoceratoidea, possess the early internal shell morphol-



ogy of this morphotype (Figures 5; 6.5, 6; Appendix 1). Additionally, our observations are consistent with the data of other authors (Shul'ga-Nesterenko, 1926; Böhmers, 1936; Miller and Unklesbay, 1943; Bogoslovskaya, 1959; Tanabe *et al.*, 1994).

*Agathiceras morphotype*.—In median section, caecum is ellipsoid with a strongly constricted base at proseptum and second septum; prosiphon is short and gently curved ventrally, and proseptum on dorsal side is short and slightly convex adapically. Second septum is convex adorally, with a retrochoanitic septal neck, and is close to proseptum on dorsal side, forming a necklike structure in median section. Siphuncle keeps a central position in first three whorls, and subsequently gradually shifts its position toward the venter. Migration of siphuncle to ventral marginal side is completed at end of fifth whorl.

Two species of *Agathiceras* examined possess the early internal shell morphology of this morphotype (Figure 6.1, 2; Appendix 1). Schindewolf (1934) and Böhmers (1936) reported similar early internal shell features in other Permian *Agathiceras*.

*Thalassoceras morphotype*.—In median section, caecum, which is preceded by short and curved prosiphon, is ellipsoid with a strongly constricted base at proseptum and second septum; proseptum on dorsal side is short, and second septum is close to proseptum on dorsal side. Siphuncle occupies a central to subcentral position in first whorl, and subsequently shifts its position gradually to the venter in the early part of second whorl.

Three taxa assigned to the Thalassoceraoidea, *Bisatoceras* sp., *Eothalassoceras inexpectans* and *Thalassoceras gemmellaroi*, possess the early internal shell morphology of this morphotype (Figure 6.3, 4; Appendix 1).

### Ceratitida

The initial chamber of *Paraceltites elegans* is circular in median section (Figure 7.1, 2). Although the caecum, prosiphon and siphuncular tube are not preserved in specimen NSM PM16215, Spinosa *et al.* (1975, text-fig. 11) described an elongate and subelliptical caecum without a conspicuous constricted base at proseptum and one short prosiphon. The proseptum resting on the dorsal side of the initial chamber wall is long and slightly convex adapically in median section. The second septum does not appear in close vicinity to the proseptum, and the siphuncle maintains a ventral position throughout ontogeny. The maximum initial chamber size, ammonitella size and ammonitella angle in NSM PM16215 are 0.463 mm, 0.921 mm and 342° respectively (Appendix 1).

The early internal shell morphology of the early Triassic ceratitid *Nordophiceras jacksoni* (Figure 7.3, 4) is similar to those observed in *Paraceltites elegans* and *Daraelites elegans* except for the much smaller ammonitella angle (264°).

### Discussion

Since the lobe development in the Prolecanitida has been thought to be identical with that in the Ceratitida, many authors have attributed the ancestor of the Ceratitida to the

Prolecanitida (Spath, 1934; Schindewolf, 1953; Ruzhencev, 1960). The oldest representative of the Ceratitida is known from the lower Middle Permian (Roadian) and is referable to *Paraceltites*, which is characterized by a thinly discoidal, widely evolute conch, round venter, a prominent ventral salient in the growth lines, and unserrated lobes (Spinosa *et al.*, 1975). Compared to the other prolecanitid ammonoid genera, the genus shares more similar features of conch and suture morphology with *Daraelites*, so that previous authors considered that *Paraceltites* evolved from a daraelitid stock in the Prolecanitida, probably *Daraelites* (Ruzhencev, 1960, 1962).

Zakharov (1984, 1988), however, showed that the lobe development of the Prolecanitida is identical with that of the Goniaticitida. He noted that the ammonoid family occurring in the Lower Permian, which shares common features of conch morphology, ornamentation and suture with *Paraceltites*, is the Eothinitidae in the Goniaticitida. *Paraceltites* and Eothinitidae both display a widely evolute conch with marginal ribs rather than nodes, round venter, and simple adult suture line. Based on these facts Zakharov (1984, 1988) suggested that *Paraceltites* evolved from the Eothinitidae, probably *Epiglyphioceras* (Zakharov, 1984, 1988). However, except for the simple adult suture line, *Daraelites* also possesses these characters. Inference of a possible ancestor of *Paraceltites* on the basis of only conch morphology and ornamentation should be avoided if other features can be utilized to resolve this ancestor-descendant problem.

The Prolecanitida and Goniaticitida each exhibit certain distinct features in their early internal shell features that can be brought to bear on this problem. Available data show that the Prolecanitida share a short and curved prosiphon, a bottle-shaped or gourd-shaped caecum without a conspicuous constricted base at proseptum in median section, long proseptra on dorsal side, a ventral siphuncle, and a relatively small ammonitella angle (328–350°). The second septum does not appear in close vicinity to the proseptum. Meanwhile, species of the Goniaticitida share a short and curved prosiphon, a subelliptical or elliptical caecum with a strongly constricted base at proseptum, short proseptra on dorsal side, a ventral siphuncle, and a relatively large ammonitella angle (352–385°). The second septum is close to proseptum on the dorsal side, forming a necklike structure in median section.

*Paraceltites elegans* has a long proseptum on the dorsal side, and the second septum does not appear in close vicinity to proseptum. The ammonitella angle is 342° in the specimen examined. These features are characteristic of early internal shell features of the prolecanitid *Daraelites elegans* rather than the Goniaticitida. These similarities of early ontogenetic shell features as well as the conch morphology of shell shape, ornamentation and sutural development strongly suggest a close phylogenetic relationship between *Daraelites* and *Paraceltites*. These observations strongly support the hypothesis of the daraelitid origin for the Ceratitida as proposed by Ruzhencev (1960, 1962).



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**Appendix 1.** List of material, and measurement data and character states of the species examined. G: *Goniatites* morphotype, E: *Epicanites* morphotype, M: *Marathonites* morphotype, N: Bogoslovskaya *et al.* (1999).

Species	Horizon	Locality	Sample
<b>Order Prolecanitida</b>			
<b>Prolecanitoidea</b>			
<i>Epicanites loeblichii</i> Miller & Furnish	Chesterian	Jack Fork Creek, Oklahoma	NSM PM16188
<i>Daraelites elegans</i> Tchemow	Artinskian	Aktasty R., South Urals	NSM PM16189
<b>Pronoritoidea</b>			
<i>Neopronorites skvorzovi</i> (Tchemow)	Artinskian	Aktasty R., South Urals	NSM PM16190
<b>Medlicottioidea</b>			
<i>Akmleria electraensis</i> (Plummer & Scott)	Wolfcampian	Buck Mountain, Nevada	NSM PM16191
<i>Artioceras rhipaeum</i> (Ruzhencev)	Artinskian	Aktasty R., South Urals	NSM PM16192
<b>Order Goniatitida</b>			
<b>Dimorphoceratoidea</b>			
<i>Girtyoceras meslerianum</i> (Girty)	Chesterian	Jack Fork Creek, Oklahoma	NSM PM16193
<i>Eumorphoceras plummeri</i> Miller & Youngquist	Chesterian	San Saba, Texas	UMUT PM19030
<i>Gatherites morrowensis</i> (Miller & Moore)	Morrowan	Gather Mt., Arkansas	UMUT PM19032
<b>Goniatitoidea</b>			
<i>Goniatites multiliratus</i> Gordon	Chesterian	Jack Fork Creek, Oklahoma	NSM PM16194
<i>Goniatites</i> aff. <i>crenistris</i> Phillip	Chesterian	Ahloso, Oklahoma	UMUT PM19019-2
<i>Goniatites choctawensis</i> Shumard	Meramecian	Clarita, Oklahoma	UMUT PM19020-2
<i>Agathiceras uralicum</i> (Karpinsky)	Artinskian	Aktasty R., South Urals	NSM PM16195
<i>Agathiceras applini</i> Plummer & Scott	L. Permian	Coleman, Texas	NSM PM16196
<b>Neoglyphioceratoidea</b>			
<i>Neoglyphioceras abramovi</i> Popow	Namurian	Menkyule R., Verkhoyansk	NSM PM16197
<i>Cravenoceras incisum</i> (Hyatt)	Chesterian	San Saba, Texas	NSM PM16198
<i>Cravenoceras lineolatum</i> Gordon	Chesterian	Lick Mountain, Arkansas	NSM PM16199
<i>Cravenoceras richardsonianum</i> (Girty)	Chesterian	Wapanucka, Oklahoma	UMUT PM19021
<b>Somoholitoidea</b>			
<i>Glaphyrites hyattianus</i> (Girty)	Desmoinesian	Okmulgee, Oklahoma	NSM PM16200
<i>Glaphyrites warei</i> (Miller & Owen)	Desmoinesian	Collinsville, Oklahoma	NSM PM16201
<i>Glaphyrites jonesi</i> (Miller & Owen)	Desmoinesian	Collinsville, Oklahoma	UMUT PM19027
<i>Glaphyrites clinei</i> (Miller & Owen)	Desmoinesian	Collinsville, Oklahoma	UMUT PM19028
<b>Gastrioceratoidea</b>			
<i>Homoceras subglobosum</i> (Bisat)	L. Namurian	Stonehead Beck, Yorkshire	NSM PM16202
<i>Arkanites relictus</i> (Quinn, McCaleb & Webb)	Morrowan	Bradshaw Mt., Arkansas	UMUT PM19029
<b>Thalassoceratoidea</b>			
<i>Bisatoceras</i> sp.	Desmoinesian	Okmulgee, Oklahoma	UMUT PM19033-1
<i>Eothalassoceras inexpectans</i> (Miller & Owen)	Desmoinesian	Okmulgee, Oklahoma	UMUT PM19036-1
<i>Thalassoceras gemmellari</i> Karpinsky	Artinskian	Aktasty R., South Urals	NSM PM16203
<b>Adrianitoidea</b>			
<i>Crimites subkrotowi</i> Ruzhencev	Artinskian	Aktasty R., South Urals	NSM PM16204
<i>Crimites elkuensis</i> Miller, Furnish & Clark	Wolfcampian	Buck Mountain, Nevada	NSM PM16205
<i>Texoceras</i> sp.	Roadian	El Capitan, Texas	UMUT PM19037-1
<b>Marathonitoidea</b>			
<i>Kargalites typicus</i> (Ruzhencev)	Artinskian	Aktasty R., South Urals	NSM PM16206
<i>Marathonites invariabilis</i> (Ruzhencev)	Artinskian	Aktasty R., South Urals	NSM PM16207
<b>Neoicoceratoidea</b>			
<i>Metalegoceras</i> sp.	Wolfcampian	Buck Mountain, Nevada	NSM PM16208
<i>Metalegoceras baylorense</i> White	Wolfcampian	Buck Mountain, Nevada	UMUT PM19035
<i>Eothinites kargalensis</i> Ruzhencev	Artinskian	Aktasty R., South Urals	NSM PM16209
<i>Paragastrioceras kirghizorum</i> Voinova	Artinskian	Aktasty R., South Urals	NSM PM16210
<i>Paragastrioceras artolobatum</i> Ruzhencev	Artinskian	Aktasty R., South Urals	NSM PM16211
<i>Uraloceras complanatum</i> (Voinova)	Artinskian	Aktasty R., South Urals	NSM PM16212
<i>Uraloceras</i> sp.	Wolfcampian	Buck Mountain, Nevada	NSM PM16213
<b>Popanoceratoidea</b>			
<i>Popanoceras annae</i> Ruzhencev	Artinskian	Aktasty R., South Urals	NSM PM16214
<b>Order Ceratitida</b>			
<b>Xenodiscoidea</b>			
<i>Paraceltites elegans</i> Girty	Roadian	Guadalupe Mts., Texas	NSM PM16215



ined. Data source: 1. Spinosa *et al.* (1975). Abbreviations: A: *Agathiceras* morphotype, D: *Daraelites* morphotype, T: *Thalassoceras* morphotype. Major taxonomic positions from

Initial chamber size (mm)		Ammonitella size angle		Length of pro-siphon	Shape of caecum in median section	Length of pro-septum (dorsal side)	Proseptum & 2nd septum (dorsal side)	Initial position of sipuncle	Morpho-type
Max.	Min.	(mm)	(deg.)						
0.426	0.393	0.870	355	Short	Bottle-shaped	Long	Separate (fairly)	Ventral	E
0.466	0.405	0.913	350	?	Bottle-shaped	Long	Separate (a little)	Ventral	D
0.645	0.578	1.147	328	Short	Gourd-shaped	Long	Separate (a little)	Ventral	N
0.633	0.550	1.250	338	Short	Bottle-shaped	Long	Separate (fairly)	Ventral	E
0.356	0.311	0.702	334	Short	Bottle-shaped	Long	Separate (fairly)	Ventral	E
0.543	0.462	0.906	368	Short	Subelliptical	Long	Close	Ventral	G
—	—	1.032	—	?	?	?	?	Ventral	?
0.416	0.370	0.833	385	?	?	Long	Close	Ventral	G
0.545	0.470	0.978	360	Short	Subelliptical	Long	Close	Ventral	G
0.566	0.533	0.995	380	?	Subelliptical	Long	Close	Ventral	G
0.541	0.483	0.996	383	Short	Subelliptical	Long	Close	Ventral	G
0.513	0.451	0.949	369	Short	Elliptical	Short	Close	Central	A
0.520	0.466	1.010	365	?	Elliptical	Short	Close	Central	A
0.522	0.476	0.927	370	Short	Subelliptical	Long	Close	Ventral	G
0.490	0.446	0.910	360	Short	Subelliptical	Long	Close	Ventral	G
0.484	0.403	0.815	368	Short	Subelliptical	Long	Close	Ventral	G
0.486	0.446	0.813	367	?	?	Long	Close	Ventral	G
0.590	0.498	1.048	370	Short	Subelliptical	Long	Close	Ventral	G
0.527	0.458	0.916	369	Short	Subelliptical	Long	Close	Ventral	G
0.535	0.470	0.920	372	?	?	Long	Close	Ventral	G
0.413	0.373	0.720	379	?	?	Long	Close	Ventral	G
0.496	0.458	0.933	367	Short	Subelliptical	Long	Close	Ventral	G
—	—	0.800?	—	?	?	?	?	?	?
0.360	0.335	0.620	358	Short	Elliptical	Short	Close	Subcentral	T
0.386	0.360	0.680	365	Short	?	Short	Close	Subcentral	T
0.365	0.338	0.694	356	Short	Elliptical	Short	Close	Subcentral	T
0.376	0.332	0.681	365	Short	Elliptical	Short	Close	Ventral	M
0.384	0.350	0.725	365	Short	Elliptical	Short	Close	Ventral	M
—	—	0.958	—	?	?	?	?	?	?
0.468	0.419	0.909	360	Short	Elliptical	Short	Close	Ventral	M
0.382	0.356	0.767	366	Short	Elliptical	Short	Close	Ventral	M
0.472	0.411	0.833	365	?	?	Short	Close	Ventral	M
0.480	0.410	0.866	365	Short	Elliptical	Short	Close	Ventral	M
0.381	0.349	0.672	372	?	?	Short	Close	Ventral	M
0.396	0.366	0.689	365	?	?	Short	Close	Ventral	M
0.413	0.377	0.736	365	?	?	Short	Close	Ventral	M
0.408	0.370	0.735	362	?	Elliptical	Short	Close	Ventral	M
0.517	0.463	0.850	371	Short	Elliptical	Short	Close	Ventral	M
0.356	0.321	0.660	352	Short	Elliptical	Short	Close	Ventral	M
0.463	0.400	0.921	342	Short <sup>1</sup>	Bottle-shaped <sup>1</sup>	Long	Separate (a little)	Ventral	D





## Taxonomy and distribution of Plio-Pleistocene *Buccinum* (Gastropoda: Buccinidae) in northeast Japan

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**Abstract.** Twelve species of *Buccinum* are recorded from the Plio-Pleistocene of northeast Japan. Two new species, *Buccinum shibatense* and *B. saitoi*, are proposed, and a total of six distributional types (Types A–Fj) are recognized among the 12 species. Three extinct species comprise the type Fj, which is endemic to the Japan Sea borderland. Type A is for species that are extinct in the Japan Sea, but are still living in the Sea of Okhotsk and Bering Sea. Type B species are known as fossils only along the Japan Sea margin, and now live in the northern Japan Sea as well as in the Northwest Pacific and the Sea of Okhotsk. Type C species have been recorded as fossils from the Pacific and the Japan Sea coasts and still live in both coasts. Type D species live only on the Pacific side, and are recorded as fossils only from there. Type E species occur as fossil and living specimens only in the Japan Sea. Species in both types A and Fj species underwent extinction owing to anoxic conditions during Pleistocene glacial episodes along the Japan Sea borderland. The type E species survived in the lower sublittoral to upper bathyal waters of the Japan Sea which had normal salinity and were oxic.

**Key words:** *Buccinum*, distribution, Pliocene, Pleistocene, taxonomy

### Introduction

*Buccinum* is a common group of gastropods which lives in cold and rather deep water around the North Pacific Ocean. Some species of *Buccinum* invaded the Arctic and North Atlantic Oceans after the opening of the Bering Strait in the late Miocene or Pliocene at 4.8–5.5 Ma (Marincovich and Gladenkov, 1999) in the same manner as did the gastropod *Neptunea* (Durham and MacNeil, 1967; Vermeij, 1991).

The modern species of *Buccinum* have been taxonomically summarized by Golikov (1980) and Tiba and Kosuge (1984). Golikov (1980) described 86 species and 6 subspecies from the world ocean while Tiba and Kosuge (1984) recorded 107 species and 9 subspecies from just the North Pacific. In another study, 68 species and 13 subspecies have been reported in and around Japan (Higo *et al.*, 1999). These differences in number of species and subspecies result mainly from the wide range of morphological variation that obscures the limits of species and subspecies in this genus. Mitochondrial DNA sequences show that the genus can be subdivided into five clades (probably equivalent to subgenera) that are nearly concordant with the characteristics of shell morphology: the *B. felis*, *B. inclytum*, *B. aniwaniwanum*, *B. middendorffi* and *B. tsubai* groups (Endo and

Ozawa, 2001).

Recently, Amano *et al.* (1996) and Amano (1997) summarized the taxonomy and distribution of Plio-Pleistocene buccinids, Ancistrolepidinae and *Neptunea*, from the Japan Sea borderland. These studies demonstrated for both Ancistrolepidinae and *Neptunea* that many species which no longer live in the Japan Sea continue to dwell in the Sea of Okhotsk and Bering Sea. These authors noted that such species suffered extinction in the Japan Sea owing to paleoenvironmental changes during the Quaternary ice ages. In order to gain further insights into this phenomenon, it is necessary to examine the distributional pattern of additional taxa. *Buccinum* is well suited to this purpose, because of its ecological similarity to Ancistrolepidinae and *Neptunea*.

Before discussing the distributional pattern of *Buccinum*, it is necessary to clarify the relationships between the species. However, since most species generally have a thin and fragile shell, it is difficult to obtain well preserved specimens. This unsettled classification of the modern species and the poor preservation of fossils preclude a taxonomic summary of this genus in northeastern Japan. In this paper, we will reexamine some well preserved Plio-Pleistocene specimens of *Buccinum* and will add two new species to the genus.

Based on our taxonomical reexamination, we also will discuss the distributional pattern of the genus.

### Materials

Fossils identified as *Buccinum* were recently collected from the following ten localities (Figure 1).

Loc. 1. Large cliff 2.2 km upstream from the mouth of Sakashi-no-sawa, Teshio Town, Hokkaido; gray siltstone; late Pliocene Yuchi Formation.

Loc. 2. Outcrop along Shichirinagahama beach about 1.5 km north to Kawajiri, Ajigasawa Town, Aomori Prefecture; greenish gray sandy siltstone; late Pliocene Nurusawa Formation.



**Figure 1.** Collecting localities of *Buccinum* (using the topographical maps of "Onoppunai," "Matsunoyama-Onsen," "Iiyama," scale 1:50,000; "Morita," "Echigo-Shimoseki," "Sugatani," "Ojiya" and "Kanazawa," scale 1:25,000 published by Geographical Survey Institute of Japan).



Loc. 3. Riverside cliff along a side creek of the Onnagawa River, about 600 m south of Housaka Bridge, Sekikawa Village, Niigata Prefecture (Loc. 4 of Amano *et al.*, 1996); siltstone; late Pliocene Kuwae Formation.

Loc. 4. Small outcrop on the Koide River about 1.1 km upstream of its mouth, Shibata City, Niigata Prefecture (Fossil locality of Amano, 1998); muddy fine-grained sandstone; late Pliocene Kuwae Formation.

Loc. 5. River bank along the Shinano River, 250 m north-east of Unoki, Ojiya City, Niigata Prefecture (Loc. 7 of Amano, 1997); conglomerate; early Pliocene Kawaguchi Formation.

Loc. 6. Riverside cliff of the Sabaishi River about 300 m east to Azamihira, Matsudai Town, Niigata Prefecture; pebble-bearing sandstone; late Pliocene Higashigawa Formation.

Loc. 7. Outcrop at Taihei, Matsudai Town, Niigata Prefecture; black mudstone; early Pliocene Kurokura Formation (upper part).

Loc. 8. Riverside cliff of the Shibumi River 400 m east of Taihei, Matsudai Town, Niigata Prefecture; black mudstone; early Pliocene Kurokura Formation (upper part).

Loc. 9. Outcrop at Kutta, Iiyama City, Nagano Prefecture; siltstone; early Pliocene Nagasawa Formation.

Loc. 10. River bank of the Saikawa River, 1.1 km upstream from the Okuwa Bridge, Kanazawa City, Ishikawa Prefecture (Loc. 12 of Amano *et al.*, 1996); fine-grained sandstone; early Pleistocene Omma Formation.

We examined all specimens stored at the Joetsu University of Education (JUE), including the above-cited specimens as well as those obtained in the following studies: Amano and Kanno (1991), Nakata and Amano (1991), Amano and Karasawa (1993), Amano (1994) and Amano and Sato (1995). In addition, specimens including types were reexamined at the following institutions and museums: Tohoku University (IGPS), Saito Ho-on Kai Museum of Natural History (SHM), University of Tsukuba (IGUT), National Science Museum (NSM), and Kyoto University (JC). Moreover, private collections of Mr. Masayuki Shimizu (Tateyama Mus.) were also examined.

In addition to our collections and those mentioned above, geographical distributions were compiled from a critical survey of the literature (Iwai, 1965; Noda and Masuda, 1968; Baba, 1990).

### Systematic description of new species

Family Buccinidae Rafinesque, 1815

Genus *Buccinum* Linnaeus, 1758

*Buccinum shibatense* sp. nov.

Figure 2. 3, 2. 6

*Type specimen*.—Holotype, JUE no. 15699, 39.7 mm high, 23.3 mm wide; Paratype, JUE no. 15700, 25.6 mm high, 24.6 mm wide.

*Type locality*.—Loc. 4.

*Diagnosis*.—Small species of *Buccinum* characterized by numerous spiral cords (36 to 40 on body whorl), two fine columellar plaits at base of inner lip, and thick outer lip weakly crenulated on inner side.

*Description*.—Shell rather small for genus, conico-ovoidal shape; protoconch one and a half smooth whorls; teleoconch of seven whorls. Height of body whorl occupying about five-eighths of shell height. Suture shallow and slightly undulating on body whorl. Axial sculpture of many fine growth lines; spiral cords low, separated by shallow grooves, 16 (holotype) and 20 (paratype) on penultimate whorl, 36 (holotype) to 40 (paratype) on body whorl. Spiral cords on body whorl with one shallow groove. Aperture ovate; inner lip covered by thin calcareous callus, two fine and distinct columellar plaits at its base; outer lip thick, with 19 weak striae along inner side, excavated behind. Siphonal canal shallow and slightly twisted; posterior sinus narrow and short.

*Remarks*.—At a glance, this species resembles *Pseudoliomesus ooides* (Middendorff, 1849) in its shell outline and slightly twisted basal part of the inner lip. It differs from *P. ooides* by lacking a deep suture or a subsutural area.

*Comparison*.—The present species is closely allied to *Buccinum habui* Tiba, 1984, now living at 400–500 m depth off southern Hokkaido (Higo *et al.*, 1999). *B. habui* is also characterized by numerous spiral cords (26 on penultimate; 44 on body whorl), one or two fine columellar plaits at the base of the inner lip, and weak crenulations in the inner side of the thick outer lip. However, *B. shibatense* can be easily distinguished from *B. habui* by its larger shell size, less slender shell outline, existence of a posterior sinus, and slightly twisted siphonal canal.

### *Buccinum saitoi* sp. nov.

Figure 2. 8, 2. 9

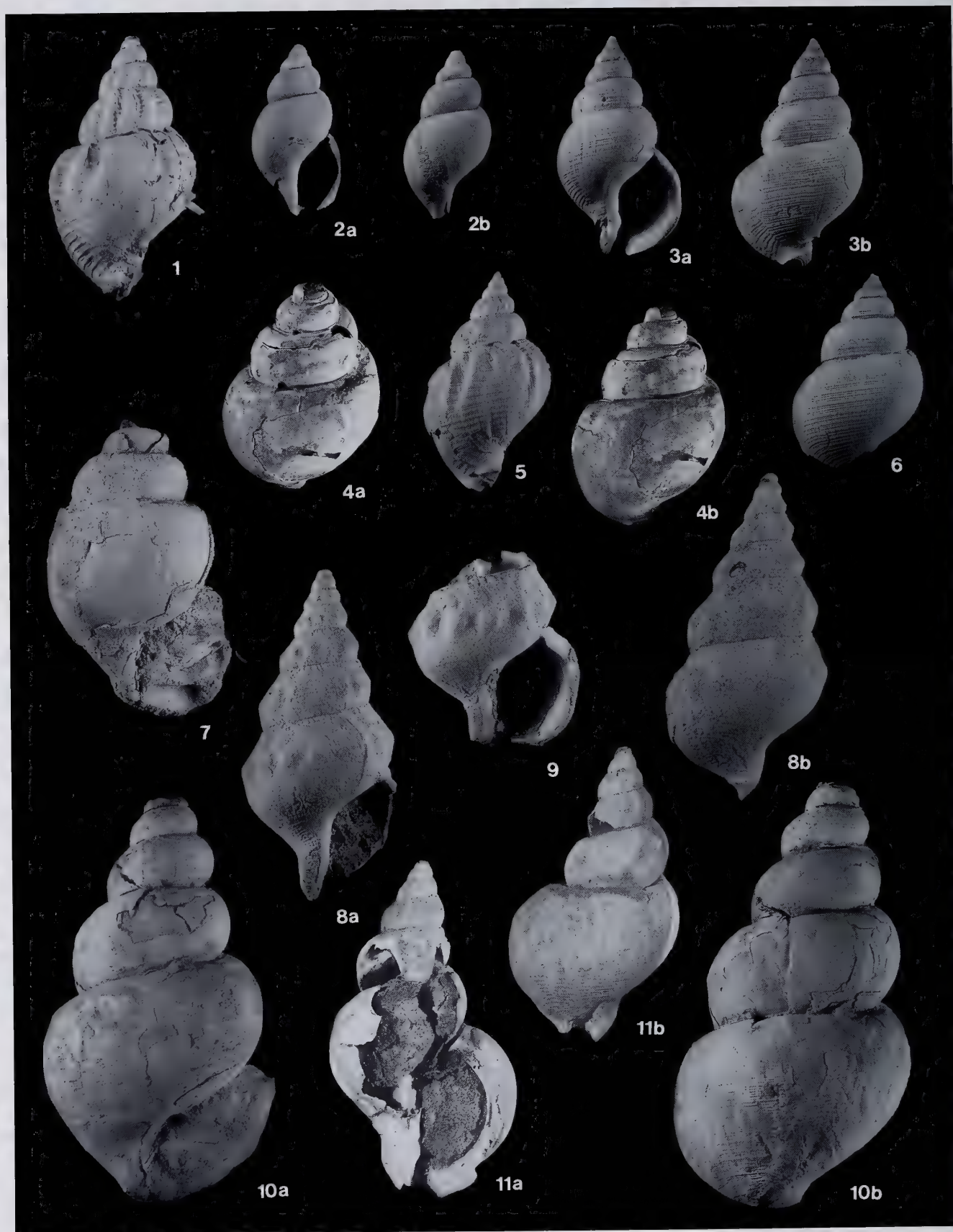
*Type specimen*.—Holotype, JUE no. 15701, 58.8+ mm high, 29.1 mm wide; Paratype, JUE no. 15702, 31.8 mm wide.

*Type locality*.—Loc. 4.

*Diagnosis*.—Medium-size *Buccinum* characterized by thick and high spire, numerous and fine subsutural granulations, distinct nodes on shoulder (13 on body whorl).

*Description*.—Shell size medium for genus, slender and thick; protoconch poorly preserved and of more than one whorl; teleoconch of six whorls. Spire rather high, occupying about half of shell height. Suture shallow and slightly undulating on body whorl, with many fine subsutural granulations. Above shoulder, 13 oblique low axial ribs; 13 distinct nodes at shouldered edge; spiral cords low, fine, separated by narrow grooves, 13 on penultimate and 15 on body whorl. Below shoulder including base, surface sculpture consisting only of spiral cords; 8 on penultimate and 25 on body whorl. Aperture ovate; inner lip covered by thin calcareous callus, nearly straight at its base; outer lip thick, smooth on inner side, excavated behind. Siphonal canal shallow; posterior sinus narrow and very short.

*Comparison*.—The present new species is closely allied to *Buccinum verrucosum* Tiba, 1980 now living in the Sea of Okhotsk. *B. verrucosum* shares the following characteristics with the present new species: similar shell outline, thick shell, many fine subsutural plications, axial ribs above the shoulder and some granulations on the shoulder. However, *B. verrucosum* differs from *B. saitoi* by having three strong





spiral cords and two obscure columellar plaits.

*Buccinum opisoplectum* Dall, 1907 can be easily distinguished from *B. saitoi* in having a smaller shell, lacking granulation on the shoulder and having three strong spiral cords.

**Etymology.**—This species is named after Mr. Atsushi Saito of Niigata Higashi High School, who collected the type specimens.

### Revision of some fossil species

*Buccinum sinanoense* was originally established by Makiyama (1927) based on the specimen (Figure 3. 4) from the early Pliocene Joshita Formation in Nagano Prefecture. Nomura (1937) illustrated a specimen as *B. sinanoense* Kuroda (?) [sic] from the Pliocene Kannonji Formation in Yamagata Prefecture. Based on an examination of his specimen, it is not referable to *B. sinanoense* because of its low and large body whorl. However, the poor preservation of its shell surface prevents us from definitely assigning this specimen to a species.

*Buccinum aomoriensis* Hatai, Masuda and Suzuki, 1961 is represented by a single specimen (Figure 3. 9) from the early Pleistocene Hamada Formation in Aomori Prefecture. This species is characterized by a large shell (shell height = 95.0 mm), many fine subsutural plications, 17 axial folds on the penultimate whorl, two strong spiral cords with two to seven intercalating cords on each whorl, and an inner lip with two columellar plaits. When they established this species, Hatai *et al.* (1961) did not compare their species with the closely related species, *B. inclytum* Pilsbry, 1904. The two species cannot be consistently distinguished, so we consider *B. aomoriensis* to be a junior synonym of *B. inclytum*.

Akamatsu and Suzuki (1992) illustrated a fragmentary specimen from the early Pleistocene Shimonoporo Formation as *Buccinum opisthoplectum* Dall [sic]. However, judging from their figure, this specimen is referable to *B. inclytum* because of its large shell (more than 50 mm without body whorl) and three rather strong spiral cords.

Hatai and Nisiyama (1952) proposed the new species *Buccinum wakimotoense* based on a specimen from the middle Pleistocene Shibikawa Formation in Akita Prefecture, which Kanehara (1942) referred to as "*B. schantaricum* Middendorff." However, they did not give a description or definition at that time. Judging from Kanehara's (1942) figure and a specimen from the Shibikawa Formation (Figure 2. 5), there is no difference between *B. wakimotoense* and the modern *B. middendorffi* Verkrüzen, 1882 as pointed out by Masuda and Noda (1976). Therefore, *B. wakimotoense* is a junior synonym of *B. middendorffi*.

*Buccinum rhodium* Dall, 1919 lives in the Sea of Okhotsk

and Bering Sea (Tiba and Kosuge, 1984). It has 22 strong sigmoid axial ribs. The specimen figured by Fujii and Shimizu (1988; Figure 3. 7) as *Plicifusus* [this should be "*Plicifusus*" cf. *plicatus* [sic] from the Pliocene Mita Formation in Toyama Prefecture has a rather large body whorl, 18 sigmoid axial ribs and 40 spiral cords. Judging from the outline and shell sculpture, their specimen is referable to *B. rhodium*. The spiral cords of modern specimens are generally weaker than on fossils.

Nomura (1937) recorded one specimen as *Ancistrolepis fragilis* Dall var. (Figure 3. 5) from the Pliocene Kannonji Formation in Yamagata Prefecture. However, it lacks a deeply channeled suture which is characteristic of Ancistrolepidinae. This specimen should be referred to *Buccinum unuscarinatum* Tiba, 1981, which lives in the Sea of Okhotsk, because of the one keel at its shoulder and many fine weak spiral cords.

*Buccinum* cf. *striatissimum* Sowerby was described by Ozaki (1958) from the Plio-Pleistocene Ilioka Formation in Chiba Prefecture. His specimen has a constricted body whorl, a large protoconch, and a deeply channeled subsutural area, all of which are characters of Ancistrolepidinae. Therefore, the Ilioka specimen is not a *Buccinum*.

*Buccinum suruganum kasimensis* was established by Ozaki (1958) as a new subspecies, based on one imperfect specimen (NSM P1 4402) from the Pliocene Naarai Formation. Based on our reexamination of this specimen, it is clear that the number of spiral cords (four cords on the penultimate whorl) and the condition of interspaces of the ribs are included in the variation of *B. leucostoma* Lischke, 1872.

When he established *Buccinum yoroianum* as a new species, Ozaki (1958) designated a small specimen (Figure 2. 2) as the paratype. However, this paratype specimen differs from the holotype in having very weak spiral cords and well inflated whorls. Based on the shell outline, size and sculpture of the paratype specimen, it is assigned to *B. bulimiloideum* Dall, 1907.

### Distributional patterns

The twelve Plio-Pleistocene species of *Buccinum* and their geological distributions in northeastern Japan are shown in Table 1. There are six types of distribution (Types A-F; Figures 4, 5).

Type A (*B. rhodium* and *B. unuscarinatum*) is for species that are extinct in the Japan Sea, but are still living at lower sublittoral to upper bathyal depths in the Sea of Okhotsk and Bering Sea. Some Ancistrolepidinae and *Neptunea* show a similar distribution (Amano *et al.*, 1996; Amano, 1997).

*Buccinum middendorffi* and *B. inclytum* belong to Type B. Fossils of these species are known only from the Japan Sea

← **Figure 2.** 1, 5. *Buccinum middendorffi* Verkrüzen. 1, x1, JUE no. 15706, Loc. 1, Yuchi Formation. 5, x1, JUE no. 15707, Loc. Anden, Akita Pref., Shibikawa Formation. 2a, b. *Buccinum bulimiloideum* Dall, x1.5, NSM no. 4464, "Paratype" of *B. yoroianum* Ozaki, Ilioka Formation. 3a, b, 6. *Buccinum shibatense* sp. nov. 3a, b, x1, JUE no. 15699, Holotype; 6, x1, JUE no. 15700, Paratype; Loc. 4, Kuwae Formation. 4a, b, 7. *Buccinum tsubai* Kuroda. 4a, b, IGUT no. 15602, Loc. Kitaubushi, Hokkaido, Yuchi Formation. 7, x1, JUE no. 15708, Loc. 6, Higashigawa Formation. 8a, b, 9. *Buccinum saitoi* sp. nov. 8a, b, x1, JUE no. 15701, Holotype; 9, x1, JUE no. 15702, Paratype; Loc. 4, Kuwae Formation. 10a, b. *Buccinum striatissimum* Sowerby, x0.8, JUE no. 15709, Loc. 8, Kurokura Formation. 11a, b. *Buccinum ochotense* (Middendorff), x0.9, IGPS no. 90462, Loc. 6 of Hatai *et al.* (1961), Hamada Formation.







**Table 1.** Distribution of the Plio-Pleistocene *Buccinum*. \* living depth after Higo *et al.* (1999).

Species	Age and formation	Depth range*
<b>Type A</b>		
<i>Buccinum rhodium</i> Dall	Pliocene Nakawatari F., Nagasawa F., Mita F.	100–300m
<i>B. unuscarinatum</i> Tiba	Pliocene Kannonji F., Kuwae F., Kurokura F. Nagasawa F., Nadachi F.	—
<b>Type B</b>		
<i>B. middendorffi</i> Verkrüzen	Pliocene Yuchi F.; Early Pleistocene Omma F.; Middle Pleistocene Shibikawa F.	0–10m
<i>B. inclytum</i> Pilsbry	Early Pleistocene Shimonoporo F., Hamada F.	0–50m
<b>Type C</b>		
<i>B. ochotense</i> (Middendorff)	Pliocene Gobanshoyama F.; Early Pleistocene Shimonoporo F., Hamada F., Daishaka F.	0–50m
<b>Type D</b>		
<i>B. leucostoma</i> Lischke	Pliocene to early Pleistocene Kazusa G.	50–600m
<i>B. bulimiloideum</i> Dall	Early Pleistocene Iio Formation	300–900m 0–50m
<b>Type E</b>		
<i>B. striatissimum</i> Sowerby	Pliocene Narusawa F., Kurokura F., Nagasawa F., Nadachi F.	200–500m
<i>B. tsubai</i> Kuroda	Pliocene Yuchi F., Kawaguchi F., Higashigawa F., Mita F.	100–700m
<b>Type Fj</b>		
<i>B. sinanoense</i> Makiyama	Pliocene Joshita F., Ogikubo F.	—
<i>B. shibatense</i> sp. nov.	Pliocene Kuwae F.	—
<i>B. saitoi</i> sp. nov.	Pliocene Kuwae F.	—

borderland. Type B species now live in the upper sublittoral zone of the northern Japan Sea as well as the Northwest Pacific and the Sea of Okhotsk.

Type C includes only one species, *B. ochotense*. This type of species is the same as the C type of *Neptunea* which has been recorded as fossils from the Pacific and the Japan Sea coasts and also lives in the upper sublittoral zone of both coasts.

Two species (type D) live only from the lower sublittoral to the upper bathyal zone on the Pacific side, and their fossils are also recorded only from the Pacific side. These are *B. leucostoma* and *B. bulimiloideum*. Such a distribution has also been observed in the buccinids *Clinopegma unicum*, *Neptunea kuroshio*, *N. fukueae* and *N. kanagawaensis* (Amano *et al.*, 1996; Baba, 1990; Kato, 1993).

Type E species (*B. striatissimum* and *B. tsubai*) are known as fossil and living specimens only from the Japan Sea. No species of *Neptunea* or Ancistrolepidinae shows this type of distribution.

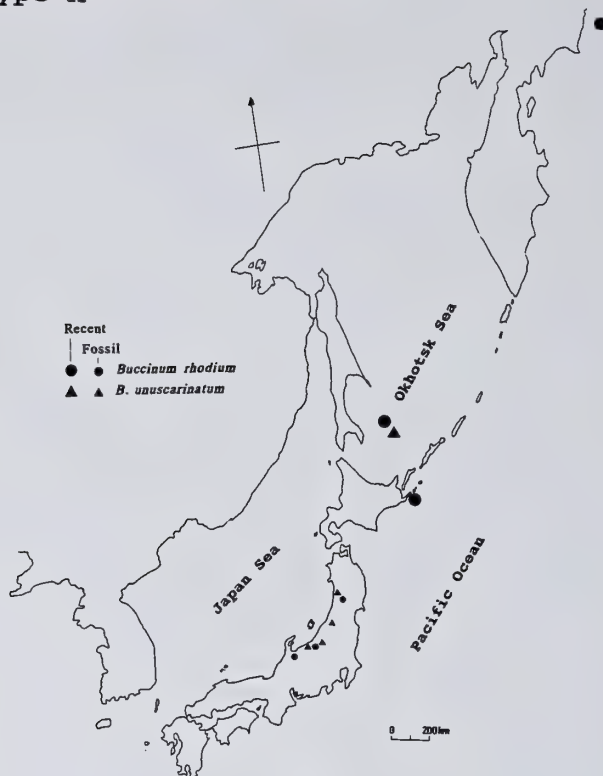
Three extinct species (*B. sinanoense*, *B. shibatense* and *B. saitoi*) comprise type Fj, endemic to the Japan Sea borderland. It is noteworthy that no extinct species of *Buccinum* is confined to the Plio-Pleistocene of the Pacific Ocean side. This type of distribution does occur in Ancistrolepidinae (Amano *et al.*, 1996) and *Neptunea* (E type; Amano, 1997).

#### Discussion of distribution

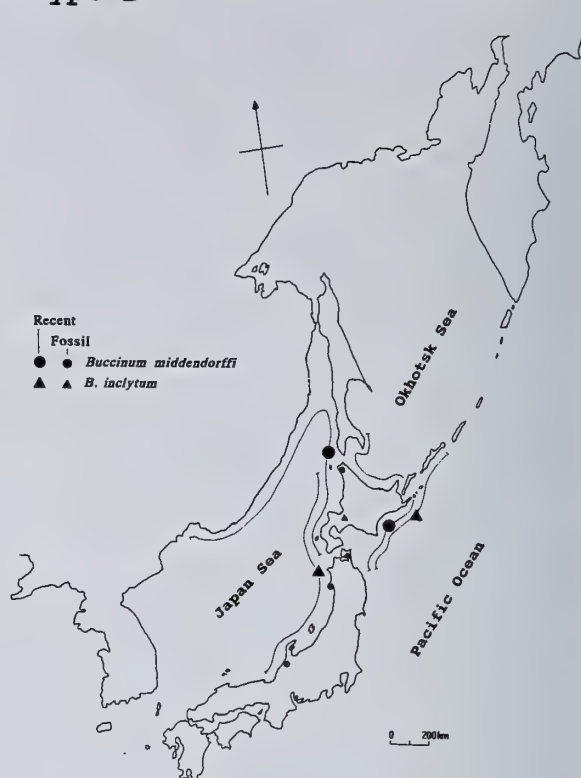
Species of types A and Fj underwent extinction during the Pleistocene in the Japan Sea borderland. Tada (1994) noted that bottom sediments alternated between oxic and anoxic conditions with the glacio-eustatic sea level changes many times after the late Pliocene. He also pointed out that remarkable sea level oscillations are recognized during the last 0.8 m.y. During the low glacial sea level stands, freshwater input reduced salinity and created euxinic conditions in the enclosed Japan Sea. The type A species occurred

← **Figure 3.** 1, 6, 7a, b. *Buccinum rhodium* Dall. 1, ×1, JUE no. 15360, Loc. N5 of Nakata and Amano (1991); 6, ×1, JUE no. 15703, Loc. 9; Nagasawa Formation. 7a, b, ×1, Loc. Rengeji, Toyama Pref., illustrated by Fujii and Shimizu (1988) as *Plicifuscus* cf. *plicatus*, Mita Formation. 2, 3, 5. *Buccinum unuscarinatum* Tiba. 2, ×1, JUE no. 15704, Loc. 7, Kurokura Formation. 3, ×0.8, JUE no. 15613, Loc. 32 of Amano and Kanno (1991), Nadachi Formation. 5, ×1, SHM no. 8407, Loc. Futago, Yamagata Prefecture, illustrated by Nomura (1937) as *Ancistrolepis fragilis* var., Kannonji Formation. 4. *Buccinum sinanoense* Makiyama, ×1, JC no. 610024, Holotype, Joshita Formation. 8. *Buccinum middendorffi* Verkrüzen, ×1, JUE no. 15705, Loc. 10, Omma Formation. 9 a, b. *Buccinum inclytum* Pilsbry, IGPS no. 90509, Hamada Formation, "Holotype" of *B. aomoriensis* Hatai, Masuda and Suzuki.

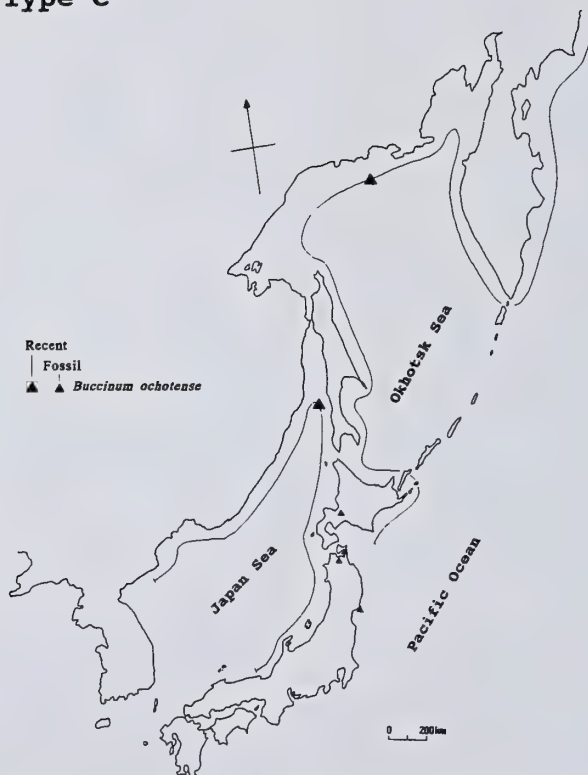
Type A



Type B



Type C



Type D

Figure 4. Distributional pattern (types A-D) of *Buccinum*.



from the lower to upper Pliocene while the type F<sub>J</sub> species ranged from the lower to middle Pliocene. Thus, it is reasonable to infer that type A species became extinct in the Japan Sea whereas the Sea of Okhotsk and Bering Sea populations survived. The narrowly distributed endemic F<sub>J</sub> type species became extinct after the late Pliocene.

Two explanations are available to explain the distribution pattern of the types B and C. First, the species of these types survived the deteriorated environment in the Japan Sea during the Quaternary ice ages. Second, the populations of species in types B and C became extinct in the Japan Sea, but survived on the Pacific side. Species of both types live in upper sublittoral depths while those of other types dwell in lower sublittoral to upper bathyal waters. Based on the presence of type A and F<sub>J</sub> species and the low-salinity surface water of the glacial age, it is reasonable to accept the second hypothesis. Thus, the modern populations of types B and C species in the Japan Sea may represent recent invasions through its shallow northern entrance.

The fossil records of the type D species are concentrated in the Pacific side of central Japan (Kanto Region). These species are also deep-water dwellers and survived the glacial episodes only in the Pacific Ocean.

Type E species that survive as endemics in the Japan Sea live in intermediate waters. As already noted by Amano (1996), *Portlandia toyamaensis* (Kuroda, 1929) also shows this type of distribution. The same pattern occurs in the buccinids *Mohnia yanamii* (Yokoyama, 1926) and *Lusivolutopsius furukawai* (Oyama, 1951). *Mohnia yanamii* is a

**Table 2.** Bathymetric distribution of the Japan Sea endemic species with fossil records. \* living depth after Higo *et al.* (1999).

Species	Depth (m)*
<i>Alvania sitta</i> (Yokoyama)	200-204
<i>Lusivolutopsius furukawai</i> (Oyama)	200-350
<i>Mohnia yanamii</i> (Yokoyama)	50-400
<i>Buccinum striatissimum</i> Sowerby	200-500
<i>B. tsubai</i> Kuroda	100-700
<i>Curtitoma exquisita</i> (Yokoyama)	300-400
<i>Propebela komakahida</i> (Otuka)	200-350
<i>P. tayensis</i> (Nomura and Hatai)	150
<i>Yoldia kikuchii</i> Kuroda	100-150
<i>Portlandia toyamaensis</i> (Kuroda)	100-600

characteristic species of the Omma-Manganji fauna (Otuka, 1939) and now lives in 50–400 m depth in the Japan Sea (Higo *et al.*, 1999). *Lusivolutopsius furukawai* is also known as an endemic species in the Japan Sea (200–350 m depth; Higo *et al.*, 1999) and there is one fossil specimen from the lower Pleistocene Sawane Formation at Tohoku University (IGPS no. 73410). Summarizing the Japan Sea endemic species that have fossil records (Table 2), all live in depths from 100 m–400 m. Horikoshi (1986) suspected that some species at an intermediate depth could survive during the Quaternary glacial ages. Based on radiolarian fossils from a core at GH-95 St 1208, off Shakotan Peninsula,

#### Type E



#### Type F<sub>J</sub>



**Figure 5.** Distributional pattern (types E, F<sub>J</sub>) of *Buccinum*.

**Table 3.** Distributional types of *Buccinum*, *Neptunea* and *Ancistrolepidinae*.  
 \*Amano (1997) \*\* Amano *et al.* (1996)

Types	<i>Buccinum</i>	<i>Neptunea</i> *	<i>Ancistrolepidinae</i> **
FJ	<i>B. sinanoense</i>	<i>N. eos</i>	<i>Ancistrolepis masudaensis</i>
	<i>B. shibatense</i>	<i>N. hataii</i>	<i>A. koyamai</i>
	<i>B. saitoi</i>	<i>N. nikkoensis</i>	<i>A. peulepis</i>
			<i>A. aff. hikidai</i>
A	<i>B. rhodium</i>	<i>N. lamellosa</i>	<i>Clinopegma fragilis</i>
	<i>B. unuscarinatum</i>	<i>N. satura</i>	<i>Ancistrolepis grammatus</i>
		<i>N. insularis</i>	<i>Clinopegma borealis</i>
		<i>N. vinosa</i>	<i>Bathyancistrolepis trochoideus</i>
B	<i>B. middendorffi</i>	<i>N. lyrata</i>	—
	<i>B. inclytum</i>	<i>N. bulbacea</i>	
		<i>N. rugosa</i>	
C	<i>B. ochotense</i>	<i>N. intersculpta</i>	—
		<i>N. arthritica</i>	
D	<i>B. leucostoma</i>	<i>N. kuroshio</i>	<i>Clinopegma unicum</i>
	<i>B. bulimiloideum</i>	<i>N. fukueae</i>	
		<i>N. kanagawaensis</i>	
E	<i>B. striatissimum</i>	—	—
	<i>B. tsubai</i>		

Hokkaido, Itaki *et al.* (1996) inferred normally saline and oxic water at depths of 200–300 m during the last glacial age (18–15 kyr BP). The inferred survival depth (200–300 m) of radiolarians is similar to that for the molluscs (100–400 m). Therefore, the endemic molluscs noted above, including type E of *Buccinum*, might have been able to survive the Quaternary glacial ages in the normal saline and oxic water lying between the brackish surface and the euxinic bottom waters.

Based on the discussion above, we synthesize the distributional pattern of *Buccinum*, *Neptunea* and *Ancistrolepidinae* in Table 3. It is noteworthy that 20 species (56%) belong to the type FJ or A, and there are no extinct species whose fossil records are confined to the Pacific side. Many authors have cited temperature change as one of the important causes of extinction (ex. Stanley, 1984). However, from the above lines of evidence, we postulate that the extinction of species was induced by environmental change in the Japan Sea accompanying the glacio-eustatic sea level changes during the Quaternary ice ages, not by sea surface temperature.

Valentine and Jablonski (1991) noted that marine invertebrate faunas that are not perched are unlikely to suffer extinction by eustatic sea-level changes alone. They also pointed out that the trapped fauna in enclosed areas are vulnerable to any local environmental deterioration. The present study reveals the mechanism of extinction associated with glacio-eustatic sea level changes in a marginal sea.

Tada (1994) illustrated the two-layer model of the Japan Sea during the glacial period with a surface brackish layer and deep anoxic water. However, the existence of type E

species in *Buccinum* suggests the possibilities of normal oceanic water between these two layers.

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- ◎第151回例会は、2002年1月26日（土）、1月27日（日）の両日にわたりに鹿児島大学理学部で開催されます。1月27日（日）午後には公開講演として「21世紀は自然史の時代 ―古生物学・フィールド科学からの提言―：世話人、森 啓・矢島道子；平成13年度科研費研究成果公開発表（B）」を実施致します。また1月26日（土）には、昨年と今年度の学術賞受賞者の特別講演6件を予定しております。一般講演の申し込み締切は2001年11月30日（金）です。
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## CONTENTS

<b>Keiichi Hayashi:</b> Ostracode biostratigraphy of the Lower Cretaceous Wakino Subgroup in northern Kyushu, Japan .....	143
<b>Tatsuro Matsumoto and Takemi Takahashi:</b> Further notes on the turrilitid ammonoids from Hokkaido-Part 2 (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-XC) .....	163
<b>Sanghamitra Ray:</b> Small Permian dicynodonts from India .....	177
<b>Ritsuo Nomura:</b> Quantification of optically granular texture of benthic foraminiferal walls .....	193
<b>Yasunari Shigeta, Yuri D. Zakharov and Royal H. Mapes:</b> Origin of the Ceratitida (Ammonoidea) inferred from the early internal shell features .....	201
<b>Kazutaka Amano and Mikiko Watanabe:</b> Taxonomy and distribution of Plio-Pleistocene <i>Buccinum</i> (Gastropoda: Buccinidae) in northeast Japan .....	215

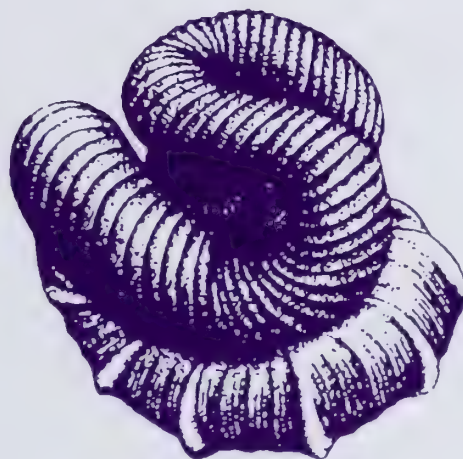


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**Cover:** Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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# A study of *Hypoturrilites* (Ammonoidea) from Hokkaido (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin–XCI)

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**Abstract.** This paper presents the result of our study on the genus *Hypoturrilites* from the Mikasa district, Central Hokkaido. *H. gravesianus* (d'Orbigny, 1842), *H. wrighti* sp. nov., *H. komotai* (Yabe, 1904), *H. yabei* Collignon, 1964 and *H. nodiferus* (Crick, 1907) are described, giving new or revised diagnoses and comparisons with other species. As to *H. komotai* the ambiguities in the previous record of occurrence are cleared up. Hence, the described species are all early Cenomanian in age. Finally the systematic allocation of *Hypoturrilites* in the Turrilitidae is discussed.

**Key words:** Cenomanian, *Hypoturrilites*, *Mariella*, *Mesoturrilites*, Mikasa, Turrilitidae

## Introduction

*Hypoturrilites* is an important genus of the Turrilitidae and more than a dozen species have been reported from various regions of the world. In Japan a magnificent specimen was described long ago under the name *Turrilites komotai* Yabe, 1904. It is nowadays referred to this genus. Recently *H. aff. mantelli* (Sharpe, 1857) and *H. primus* Atabekian, 1985 have been reported to occur in the lower Cenomanian of the Shuparo Valley, central Hokkaido (Matsumoto, 2000).

In this paper materials from the Mikasa district are studied. The Cenomanian rocks exposed in the Ikushunbetsu Valley of this district represent a generally shallower facies in comparison with those in the Shuparo Valley. As to the Cenomanian stratigraphy in the type section of this area readers may refer to the note by Matsumoto (1991, p. 3–5, 21–24). A supplementary note is given to a particular case concerned.

The materials of this study depend primarily on the collection of T. T. with an addition by Tamotsu Omori. The described specimens are to be held in the Kyushu University Museum with registered numbers under the abbreviated heading GK. One specimen of UMUT [the University Museum, the University of Tokyo] described by Yabe (1904) is restudied.

For brevity the following abbreviations are used in the description: D = diameter, B = breadth and H = height of the preserved last whorl; d = diameter of the whorl preceding the last one, h = height of the exposed outer face of the same whorl as above.

## Systematic descriptions

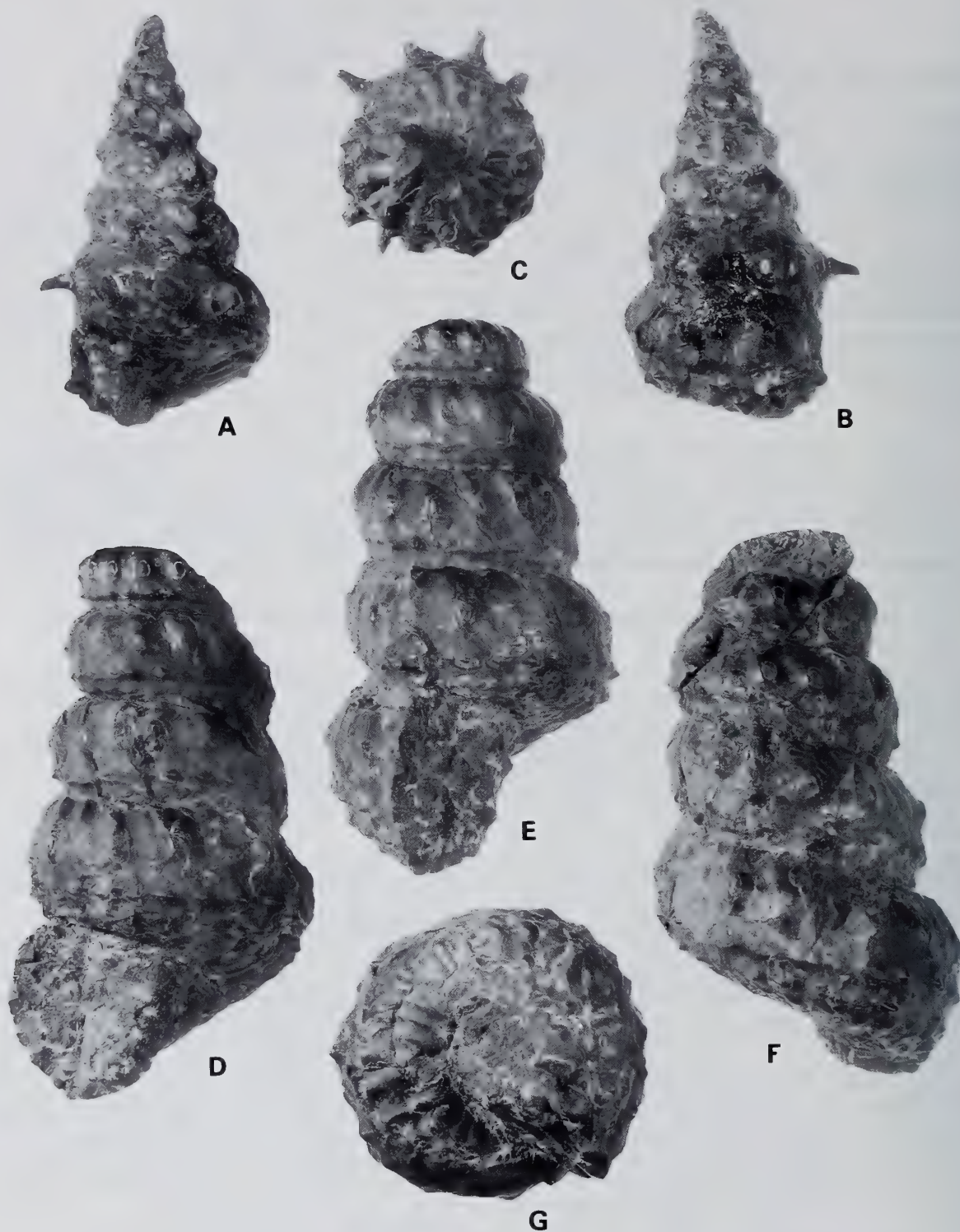
Order Ammonoidea Zittel, 1884  
Suborder Ancyloceratina Wiedmann, 1966  
Superfamily Turrilitoidea Gill, 1871  
Family Turrilitidae Gill, 1871  
Genus *Hypoturrilites* Dubourdieu, 1953

*Type species.*—*Turrilites gravesianus* d'Orbigny (1842, p. 596, pl. 144, figs. 3–5) by original designation (Dubourdieu, 1953, p. 44).

*Diagnosis.*—More or less large, sinistrally coiled turreted shell, with high or low apical angle. Whorls in tight contact, showing convex flanks and deeply impressed interwhorl junction. Each whorl ornamented by a first row of major tubercles at about midflank and closely set second and third rows of more numerous, spirally elongated minor tubercles in the lower part of the flank. The basal surface of the whorl ornamented by radial ribs, with minor tubercles of a fourth row on its margin. Septal suture highly indented, with L at about the concave zone below the row of major tubercles. Elongated branches of the inner element (I) extend to the zone of L (see Figures 2, 7; also Atabekian, 1985, pl. 23, fig. 1).

*Discussion.*—The systematic position of *Hypoturrilites* in the Turrilitidae is debatable. We intend to discuss this problem after completing the descriptions of species.

*Occurrence.*—This genus is widespread in the lower Cenomanian of Europe (except for Northern Europe), West and Central Asia, the Middle East, North Africa, South Africa, Madagascar, South India, North Australia, New



**Figure 1.** A–C. *Hypoturritilites gravesianus* (d'Orbigny, 1842). Two lateral (A and B, 180° apart each other) and basal (C) views of GK. H8543,  $\times 1.5$ . D–G. *Hypoturritilites wrighti* sp. nov. Three lateral (D, E and F, 90° apart successively) and basal (G) views of GK. H8544 (holotype),  $\times 1.25$ . Photos courtesy of M. Noda.



Zealand, Japan, Mexico and the U. S. Gulf Coast and Argentina. It seems to range upward to the middle Cenomanian in North Australia and North Africa (Wright and Kennedy, 1996, p. 364).

***Hypoturrilites gravesianus* (d'Orbigny, 1842)**

Figure 1A-C

*Turrilites tuberculatus* Mantell, 1822, p. 124 (*pars*), pl. 24, fig. 6.

*Turrilites gravesianus* d'Orbigny, 1842, p. 596, pl. 144, figs. 3-5.

*Hypoturrilites gravesianus* (d'Orbigny). Dubourdieu, 1953, p. 44;

Wright and Kennedy, 1996, p. 364, pl. 102, fig. 10; pl. 105, figs.

1-6; pl. 110, figs. 2, 8, 9; pl. 111, fig. 6; pl. 112, figs. 1, 3; pl. 113,

figs. 1, 2, 5, 7, 10-12; text-figs. 134R; 140J, R; 141E; 145F;

147E-G (with full synonymy).

**Type.**—The complex status of the type material of this species is explained in detail by Wright and Kennedy (1996, p. 365) and not repeated here. We agree with them in their proposal to designate BMNH C5726b as the lectotype of this species. It was illustrated by Mantell (1822, pl. 24, fig. 6) under *Turrilites tuberculatus*, but it is a well preserved syntype of d'Orbigny's species (Wright and Kennedy, 1996, pl. 113, fig. 10). We support them (Wright and Kennedy, 1996, p. 363) in favour of their application to the International Commission to designate *T. gravesianus* d'Orbigny instead of *T. giganteus* Haan, 1825 (p. 75) as type species of *Hypoturrilites*.

**Material.**—GK. H8543 [= previous S.36-5-14] (Figure 1A-C) collected by T. T. in 1951 at Loc. Ik1054 of the Ikushunbetsu River, from the *Mantelliceras japonicum* Zone.

**Description.**—This specimen is small and probably represents a young shell which corresponds to the unpreserved early part of the lectotype. Although the shell is destroyed at its top, the apical angle is roughly estimated as about 20°. The specimen preserves seven whorls which are in tight contact, showing a deeply impressed interwhorl junction. The flank of the whorl is convex and its height is less than half of the whorl diameter ( $h/d = 0.43$ ).

Each whorl is ornamented by a row of large, rounded tubercles at about midflank and two rows of small, somewhat clavate tubercles in the lower part immediately above and also along the lower whorl seam. There are rounded small tubercles of a fourth row on the marginal zone of the basal surface. The large tubercles number 10 to a whorl and the small ones of each row 20. A rib arises from each of the small tubercles of the fourth row and runs further on the basal surface to the umbilicus. In this specimen the rib is faintly swollen at the edge of the umbilicus. Some of the midflank large tubercles preserve a horizontally extended spine. The spine is septate at the domelike base.

Suture is not exposed on this specimen.

**Comparison.**—This specimen is identified with *H. gravesianus* because of the conformity in shell form and ornamentation with the lectotype and other examples illustrated by Wright and Kennedy (1996).

**Occurrence.**—As for material. In contrast to the abundant occurrences of this species in the Lower Chalk of southern England, number of examples is, so far, very few in Japan.



**Figure 2.** *Hypoturrilites wrighti* sp. nov. Suture of GK. H8544 (holotype) on the exposed flank at  $h = 13.0$  mm. Broken line = approximate position of whorl seam; dotted line = outline of tubercle and rib; E = external lobe; L = lateral lobe; U = umbilical lobe. Figure is about  $\times 4$ . Drawing by T. M.

***Hypoturrilites wrighti* sp. nov.**

Figures 1D-G; 2

**Holotype.**—GK. H8544 [= previous S.51-6-26] (Figure 1D-G) collected by T. T. in 1976 from a transported nodule of the seventh branch [= Shichino-sawa] of the Kami-ichino-sawa in the Ikushunbetsu Valley. The lithology and associated species of the nodule suggest a derivation from the *Mantelliceras japonicum* Zone.

**Specific name.**—In honour of C. W. Wright who has accomplished a revised systematics of the Cretaceous Ammonoidea in addition to a number of other palaeontological contributions.

**Diagnosis.**—Turreted shell with a rather small apical angle (about 20°) and tuberculate ornament like that of *H. gravesianus* and *H. tuberculatus* (Bosc, 1801), but intermediate in the number of tubercles between them. A distinct rib extends upward from each major tubercle.

**Description.**—This specimen is of moderate size, with  $D = 40$  mm and  $H = 43$  mm. It shows four whorls but lacks younger whorls and also the last part.

The whorls are in tight contact, showing a deeply impressed interwhorl junction. The outer, exposed whorl face is convex and the whorl section is subcircular ( $B/H = 0.92$ ). The height of the flank is slightly less than half of the diameter ( $h/d = 0.47$ ).

The whorl is ornamented by a first row of large tubercles at about the midflank, and three closely set rows of small tubercles in the lower part. The second row is slightly above and the third row just along the lower whorl seam; a fourth row is on the marginal zone of the basal surface of the whorl. The small tubercles of the second and third rows are spirally elongated, forming ridges which are separated by a narrow groove. On the basal surface radial ribs run with a gentle curvature from the tubercles of the fourth row toward the narrow umbilicus. In the upper part of the exposed whorl face a distinct rib extends upward from each major tubercle.

The number of tubercles per whorl increases slightly with growth. In the middle growth stage it is 15 or 16 for the row of large tubercles and 24 or 25 for each row of small tubercles.

Septal sutures are partly exposed, showing fairly narrow L





**Figure 3.** *Hypoturrillites komotai* (Yabe, 1904). Lateral (A) and basal (B) views of UMUT MM7458,  $\times 0.6$ . Photos courtesy of M. Noda.



in the zone between the first and second rows of tubercles (Figure 2). They are fine and deeply incised even on the preserved early whorls. The septa seem to be distantly separated. On the interspace between the two sutures, a branch of an inner element extends outward to the zone of L.

**Comparison.**—The holotype of this species is generally similar to *Hypoturrilites gravesianus* and *H. tuberculatus* (Bosc, 1801) (redefined by Wright and Kennedy, 1996, p. 367). The number of large tubercles per whorl is about 10 to 12 in *H. gravesianus* and 20 or so in *H. tuberculatus*. It is 15 or 16 in *H. wrighti*. This number may vary to some extent, but the above difference is beyond that extent. In *H. gravesianus* and *H. tuberculatus* the upper part of the exposed whorl face is smooth, whereas in this species a distinct rib extends upward from the large tubercle.

**Occurrence.**—As for material. At present this species is represented by a single specimen. More material should be searched out to know clearly the stratigraphic range and geographical distribution of this species.

### *Hypoturrilites komotai* (Yabe, 1904)

Figure 3

*Turrilites komotai* Yabe, 1904, p. 7, pls. 1 and 2.

*Hypoturrilites komotai* (Yabe, 1904). Collignon, 1964, p. 44, pl. 328, fig. 1468; Wright and Kennedy, 1996, p. 367, text-fig. 145C.

**Holotype.**—UMUT MM7458 (Figure 3A, B), by monotypy, collected by Komota and described by Yabe (1904). Its original locality is questionable (see occurrence).

**Diagnosis.**—A species of *Hypoturrilites* characterized by a very large apical angle and a low ratio of flank height to diameter in each whorl, which is ornamented by spinose large tubercles of the upper row and numerous small tubercles of the lower three rows. On the basal surface of the whorl ribs run obliquely to the umbilicus.

**Description.**—The holotype is very large. It consists of four whorls, and several whorls of the early growth stage are not preserved. The last whorl, with  $D = 184$  mm, is the body chamber, although its apertural part is destroyed. The estimated apical angle is as high as 70°. Whorls are in tight contact; the ratio of flank height to diameter is very low ( $h/d = 0.34$ ), while the cross section of the last whorl is subelliptical, with breadth slightly larger than height ( $B/H = 1.11$ ). The umbilicus is fairly narrow.

The outer exposed whorl face shows a nearly flat and gently inclined upper portion and a convex main part. The latter is ornamented by a first row of large tubercles, numbering 18 or 19 per whorl. In the lower part of the exposed whorl face somewhat above and along the lower whorl seam, there are the second and the third rows of small, obliquely or spirally elongated tubercles, numbering 35 or so per whorl in each row. From the small tubercles of a fourth row on the margin of the basal surface distinct ribs run to the umbilical margin with a gentle curvature (Figure 3B). The large tubercles of the first row originally had a spine which stretched laterally with a slightly upward curvature (see Yabe, 1904, pl. 1). One of us (T. M.) actually observed the spinose tubercles when he was a student at the University of

Tokyo (in 1935), but later the spines were all broken and lost. At present the exposed top of a dome-shaped large tubercle preserves the septate base of the spine (Figure 3A). The holotype does not clearly show the suture, as it is covered by a dark-colored shelly layer.

We have not observed the specimen from Madagascar, but it is identified with this species on the basis of the general conformity in the estimated apical angle and number of large tubercles, as shown by Collignon (1964, p. 44, pl. 328, fig. 1468) and also by Wright and Kennedy (1996, p. 367, text-fig. 145C). It is small and probably immature because its preserved last whorl is still septate. The suture was not drawn by these authors.

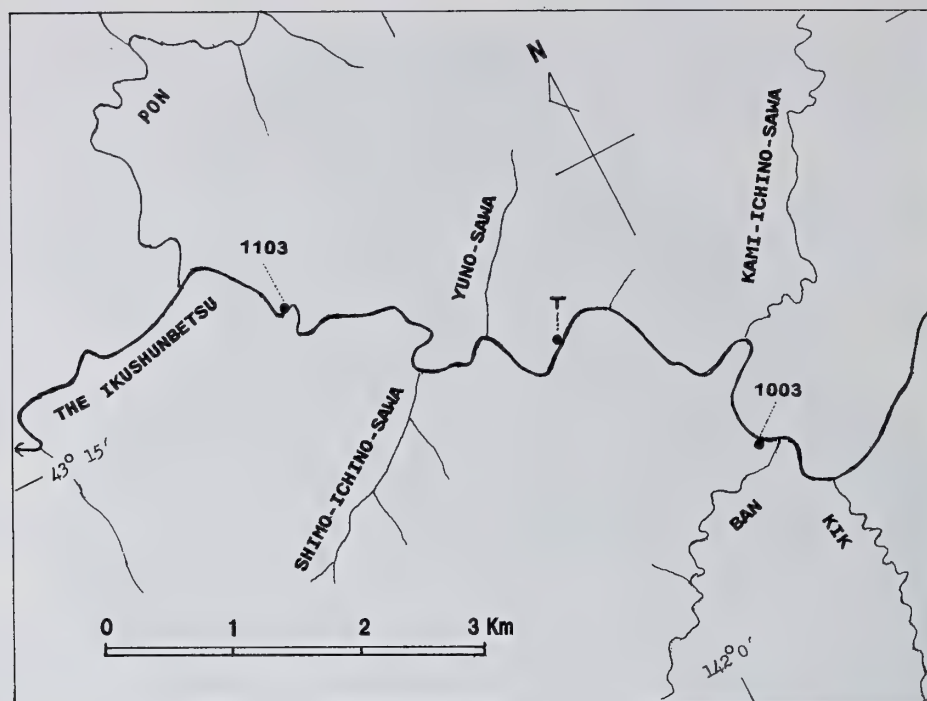
**Comparison.**—This species has diagnostic characters (*vide supra*), which enable us to distinguish it from other species. Comparison with *H. yabei* Collignon, 1964 is made below.

**Occurrence.**—Yabe (1904, p. 9) cited Komota's information that the holotype came from a loose marly nodule found below a cliff of the River Ikushunbetsu, directly upstream from the Coal Mine of Ikushunbetsu.

The above record is, however, questionable from the stratigraphic point of view. The cliff is a part of our Locality Ik1103 (Figure 4) and has yielded numerous specimens of *Calycoceras* (*Newboldiceras*) *asiaticum* (Jimbo). In fact it is the type locality of "*Acanthoceras rhotomagense* var. *asiatica*" of Jimbo (1894, p. 177, pl. 20, fig. 1). This fossiliferous part belongs to the Abundance Zone of *Calycoceras* (*Newboldiceras*) *asiaticum* in the present sense. At Loc. Ik1103 the beds with *C. (N.) asiaticum* are underlain by another fossiliferous sequence from which T. T. obtained a specimen of *Cunningtoniceras* (Matsumoto *et al.*, 1969, pl. 33, fig. 2). Thus, the fossiliferous beds of Loc. Ik1103 are as a whole referred to the middle Cenomanian. They belong to the Mikasa Formation on the western wing of the Ikushunbetsu Anticline in our present knowledge. Long ago this part was called "the Lower *Acanthoceras* zone of the *Trigonia* Sandstone" and was thought to be underlain by the "Lower Ammonite Beds" (Yabe, 1903, p. 8). Incidentally, the Upper *Acanthoceras* Zone at that date was the *Mammites*-bearing bed of an early Turonian age exposed in the Yubari Mountains.

In our present knowledge a fault of considerable magnitude is presumed to run on the east side of Ik1103 (see Matsumoto *et al.*, 1964, fig. 7) and middle Albian *Lyelliceras*-bearing strata of the Lower Yezo Subgroup are exposed for some distance (see Matsumoto, 1988, p. 157–158). Further upstream on the eastern wing of the Ikushunbetsu Anticline the successive ammonite zones in the middle part (i. e., the Member IIb) of the Mikasa Formation are exposed. They are in ascending order as follows (Matsumoto *et al.*, 1969; Matsumoto, 1991):

- (1) Assemblage Zone of *Mantelliceras japonicum*-*Sharpeiceras kongo*: middle part of the lower Cenomanian.
- (2) Ammonite-poor part, in which *Acomposoceras renevieri* (Sharpe, 1857) was found by T. T. (Matsumoto and Takahashi, 1992): upper part of the lower Cenomanian.
- (3) Subzone of *Cunningtoniceras takahashii* and Subzone of *Calycoceras* (*Newboldiceras*) *orientale*: middle Cenomanian.



**Figure 4.** Outline map of the Ikushunbetsu Valley (part). The locations of Ik1103 and Ik1003 are shown. Regrettably Ik1003 (type locality of *Reesidites minimus*) was misprinted as Ik1103 in the paper by Matsumoto (1965, fig. 2 and explanation of pls. 14 and 15), but was correctly printed in figs. 4 and 34 of the same paper. For the geology of the mapped area see Yoshida and Kanbe (1955) and Matsuno *et al.* (1964), in the latter of which the distribution of the Mikasa Formation is clearly shown (Matsuno *et al.*, 1964, fig. 7). Abbreviations in this Figure: BAN = Banno-sawa, KIK = Kikumezawa, PON = R. Ponbetsu, T = type locality of the *Mantelliceras japonicum* Zone. Put Ik at the heading of 1003 and 1103.

The Zone of *M. japonicum* is prolific and several species of *Hypoturrilites* have been collected from this zone. Recently *H. cf. komotai* has been found in the same zone at a locality of the Ganseki-zawa, i. e. the 8th branch of the Kami-ichino-sawa, about 7 km northeast from the type outcrop (indicated as T in Figure 4) of this zone.

The Mikasa Formation on the eastern wing consists mainly of sandstones and forms a ridge on the northwest side of the Kami-ichino-sawa and also another ridge on the southeast side of the Shimo-ichino-sawa (Figure 4). There is, thus, a high possibility that Komota's nodule originated from the *M. japonicum* Zone of the Mikasa Formation exposed along the Shimo-ichino-sawa and was transported downstream for about 1.5 or 2 km.

In Madagascar *H. komotai* is recorded from the lower Cenomanian (Collignon, 1964, p. 44).

#### ***Hypoturrilites yabei* Collignon, 1964**

##### Figure 5

*Hypoturrilites yabei* Collignon, 1964, p. 44, pl. 328, fig. 1469; Wright and Kennedy, 1996, p. 367, text-fig. 145D.

**Holotype.**— Original of Collignon, 1964, p. 44, pl. 328, fig. 1469 (by original designation), from the lower Cenomanian of Antanimanga of Madagascar. It is now housed in the col-

lection of the Département des Sciences de la Terre, Université de Bourgogne, Dijon (France).

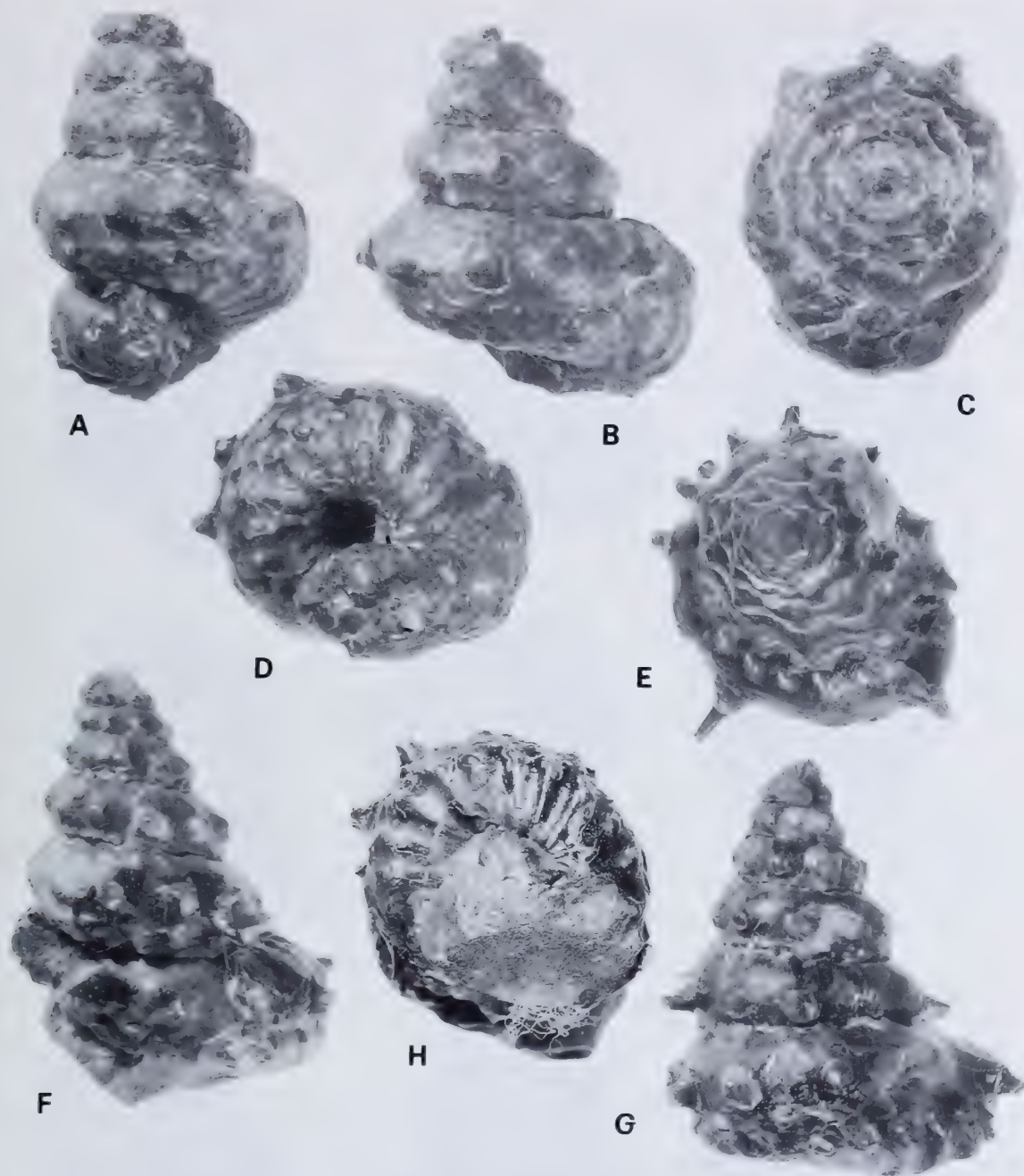
**Material.**— GK. H8545 [= previous S. 40-9-4A] (Figure 5A-D) and GK. H8546 [S. 40-9-4B] (Figure 5B-H) collected by T. T. in 1960 at Loc. Ik1100, abandoned pit on the right side of the River Ikushunbetsu; also GK. H8528 collected by Tamotsu Omori (no. 86) from the Shimo-ichino-sawa, a branch of the Ikushunbetsu. They came from the fossiliferous sandstones referred to the *Mantelliceras japonicum* Zone of the Mikasa Formation.

**Description.**— The three specimens are smaller than the holotype. The apical angle is moderate, i. e., around 50°, and h/d is rather low, 0.40–0.42. Whorls are tightly in contact and the interwhorl junction is deeply impressed. The outer exposed whorl face is convex. The umbilicus is narrow.

Each whorl is ornamented by an upper row of large tubercles at the most convex midflank and more or less spirally elongated small ones of three closely set rows in the lower part. The large tubercles number 12–13 per whorl and the small ones in each row are nearly twice as numerous as the large ones. The large tubercle has a horizontally elongated spine as shown by GK. H8546 (Figure 5E, G), but in many cases the spine is absent and its septate base is exposed, forming a rounded domelike outline (Figure 5A, B).

A shallowly concave zone may be discernible below the





**Figure 5.** *Hypoturrilites yabei* Collignon, 1964. **A-D.** GK. H8545, two lateral (A and B about 180° apart), apical (C) and basal (D) views. **E-H.** GK. H8546, two lateral (E and F about 180° apart), apical (G) and basal (H) views. Figures are all  $\times 1.25$ . Photos courtesy of M. Noda.

first row of large tubercles and a narrow spiral groove runs between the second and third rows of clavate tubercles. The tubercles of a fourth row are less clavate and situated at the curved outer edge of the basal rib.

There are short riblets on the uppermost part of the flank above the zone of large tubercles. They are roughly twice as numerous as the large tubercles.

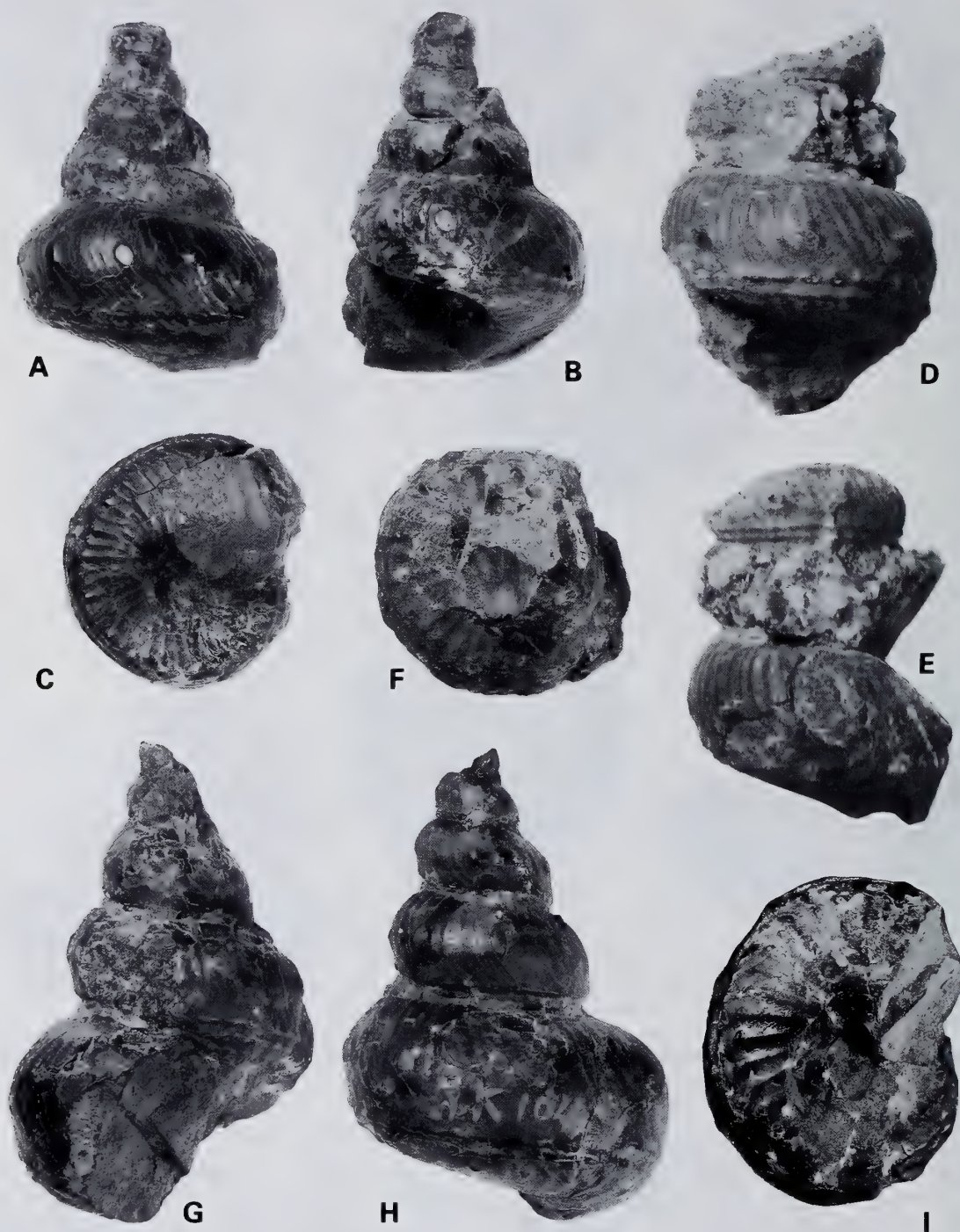
The septal suture is partly exposed on a later whorl of GK. H8546. The stem of the E-L saddle is broad, whereas L is narrow and deep, resting on the zone between the first and second rows of tubercles. The extra branch exists but is not well traced.

*Comparison.*—The described specimens are undoubtedly identified with *H. yabei* Collignon, 1964. This species is al-

lied to but distinguished from *H. komotai* by its somewhat smaller apical angle and less numerous tubercles. The uppermost row of riblets is faintly shown in the illustration by Collignon (1964, pl. 328, fig. 1469), although the author

made no mention of this character.

*Occurrence.*— As for material. Despite the long distance, *H. yabei* and *H. komotai* both occur in Japan and Madagascar. In Madagascar the two species have been re-



**Figure 6.** *Hypoturrillites nodiferus* (Crick, 1907). **A–C.** GK. H8547, two lateral (A and B about 180° apart) and basal (C) views,  $\times 1.5$ . **D–F.** GK. H5570, two lateral (D and E about 90° apart) and basal (F) views, Slightly reduced ( $\times 0.95$ ). **G–I.** GK. H5917, two lateral (G and H about 120° apart) and basal (I) views,  $\times 1.25$ . Photos courtesy of M. Noda.



corded from the same bed (Collignon, 1964, p. 44–45).

***Hypoturrilites nodiferus* (Crick, 1907)**

Figures 6, 7

*Turrilites nodiferus* Crick, 1907, p. 177, pl. 11, fig. 5, 5a.

*Turrilites tuberculatoplicatus* Seguenza var. *tenouklensis* Pervinquier, 1910, p. 57, pl. 5, fig. 31.

*Hypoturrilites nodiferus* (Crick, 1907). Klinger and Kennedy, 1978, p. 22, pl. 4, fig. 1; Collignon, 1964, p. 44, pl. 328, fig. 1466; Wright and Kennedy, 1996, text-fig. 145E.

*Hypoturrilites tenouklensis* (Pervinquier, 1910). Marcinowski, 1980, p. 261, pl. 4, fig. 17; Atabekian, 1985, p. 61, pl. 28, figs. 1, 2.

*Hypoturrilites laevigatus* (Coquand, 1862). Wright and Kennedy, 1996 (*pars*), p. 373, pl. 102, fig. 2; text-fig. 146K–M (*non* 146P, Q).

**Holotype.**—Original of Crick, 1907, p. 177, pl. 11, fig. 5, 5a, BMNH C18749, by monotypy.

**Material.**—GK. H8547 [= previous S. 51.9.25] (Figure 6A–C) collected by T. T. in 1976 from a transported nodule of the Ganseki-zawa [= the 8th branch of the Kami-ichino-sawa]; GK. H5570 [= previous S. 39.6.16] (Figure 6D–F) collected in 1954 by T. T. at Loc. Ik1101; GK. H5917 [= purchased, no. A003-17] (Figure 6G–I) from Loc. Ik1049; the latter two specimens were collected in situ. The three specimens belonged to the *Mantelliceras japonicum* Zone, lower part of the Member IIb of the Mikasa Formation.

**Description.**—The apical angle is moderate, about 40°. The whorls are in tight contact, showing a deep junction. Each whorl has a convex flank and is subcircular in cross section.

The tubercles are in four rows as in the above-described species of *Hypoturrilites*. The first row of large tubercles, 10 to 14 per whorl, is at about or slightly below the midflank. On the exposed whorl face there are numerous transverse ribs, which are individually variable in density and number, ranging from 30 to 40 per whorl. They are weakened but run adorally across the shallowly concave zone below the

row of large tubercles. Slightly above and just along the lower whorl seam there are the second and third rows of clavate, minor tubercles. They form the spiral ridges, with a narrow but distinct groove between them. The small tubercles of the fourth row are on the marginal zone of the basal surface, where radial ribs run to the umbilicus. The tubercles in each of the lower rows are approximately as numerous as the transverse ribs, but the exact correspondence in number may not be maintained as is shown on an undestroyed part of GK. H5570 (Figure 6D) and on the well preserved specimen from Madagascar (Wright and Kennedy, 1996, text-fig. 145D). The radial ribs on the basal surface are exactly as numerous as the small tubercles of the fourth row. Often a narrow riblet extends obliquely upward from the fourth tubercle to the third one.

The septal suture (Figure 7) is similar to that of other species of *Hypoturrilites*.

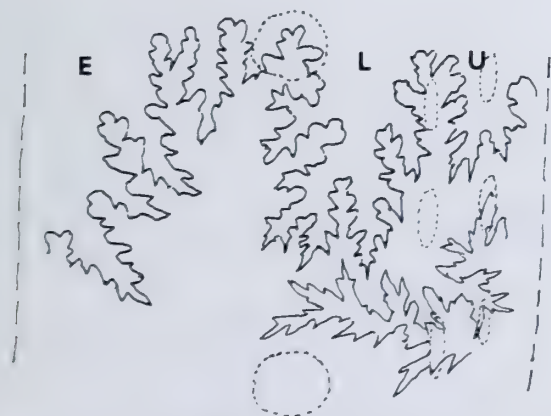
**Comparison and discussion.**—As there are some ambiguous points in some of the previously described taxa, discussion is given along with comparison. The holotype of this species from South Africa is represented by a single whorl. It was described at length by Klinger and Kennedy (1978, p. 22, pl. 4, fig. 1), but they did not mention clearly the tubercles of the fourth row, which Crick (1907, p. 177) did mention and one of us (T. M.) confirmed on the original specimen. On the weathered part or when the lighting is inadequate, the small tubercles of the fourth row are scarcely discernible. This species is represented by a better preserved specimen of Collignon (1964, p. 44, pl. 328, fig. 1466; Wright and Kennedy, 1996, text-fig. 145E) from Madagascar.

The holotype of *Turrilites tuberculatoplicatus* Seguenza var. *tenouklensis* Pervinquier (1910, p. 57, pl. 14, fig. 31) (reillustrated by Wright and Kennedy, 1996, text-fig. 146K–M), from the lower Cenomanian of Algeria, was referred to *H. laevigatus* (Coquand, 1862) by Wright and Kennedy (1996, p. 373). In our view it should be regarded as an example of *H. nodiferus* because of the resemblance in essential characters.

The holotype of *Turrilites laevigatus* Coquand (1862, p. 175, pl. 2, fig. 6) (reillustrated by Wright and Kennedy, 1996, text-fig. 146P, Q) is too much worn for the accurate definition of the species. It is estimated to have a taller shell shape with a higher h/d and a smaller apical angle in comparison with *H. tenouklensis* [= *H. nodiferus*].

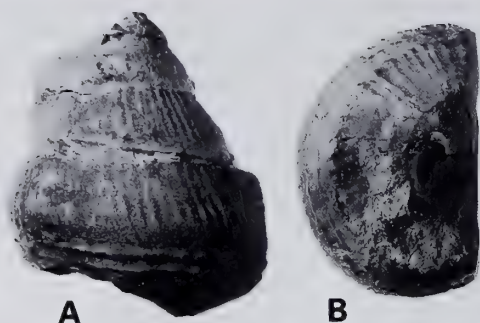
The specimen from Crimea (Ukraine) which was identified with *H. tenouklensis* by Marcinowski (1984, p. 261, pl. 4, fig. 17) undoubtedly shows three rows of small tubercles. It is probably another example of *H. nodiferus*. *H. tuberculatoplicatus* (Seguenza, 1882, p. 53, pl. 5, fig. 3), from the lower Cenomanian of Italy and England (Wright and Kennedy, 1996, p. 374, pl. 102, fig. 7; pl. 113, figs. 2, 6, 8, 9), has three rows of small tubercles as in *H. nodiferus*. It shows, however, a much taller shell shape with smaller apical angle and a higher value of h/d in comparison with *H. nodiferus*. In this respect, one of the British specimens illustrated by Wright and Kennedy (1996, pl. 113, fig. 4) might be *H. nodiferus* rather than *H. tuberculatoplicatus*.

If the large tubercles are excluded, *H. nodiferus* is considerably similar to *Mesoturrilites corrugatus* Wright and Kennedy (1996, p. 348, pl. 98, figs. 4, 17), from the lower



**Figure 7.** *Hypoturrilites nodiferus* (Crick, 1907). Suture of GK. H5570 on the flank at h = 14 mm. Legend as for Figure 2. Figure is about  $\times 3$ . Drawing by T. M.





**Figures 8.** *Mesoturrilites* aff. *corrugatus* Wright and Kennedy, 1996. Lateral (A) and basal (B) views of GS. G260,  $\times 1$ . Photos courtesy of M. Noda.

Cenomanian of England. In the same respect, we notice an interesting specimen (Figure 8) in the recent collection of Y. Kawashita (YKC111019) (registered at Saga University GS. G260) from the lower Cenomanian part of the Mikasa Formation in the Ganseki-zawa. It is tentatively called *Mesoturrilites* aff. *corrugatus*, for its ribs and small tubercles in three rows are more numerous than those of the British specimens. As to the rib density, however, there may be variation with growth and also between individuals. At any rate, this specimen (GS. G260) resembles GK. H8517 of *H. nodiferus*, if the large tubercles of the latter are ignored. Some of the transverse ribs are strengthened at or below the midflank in this specimen (GS. G260), if not forming tubercles as in *Mesoturrilites serpuliforme* (Coquand, 1862, p. 175, pl. 2, fig. 7) (see also Wright and Kennedy, 1996, p. 348, pl. 98, fig. 10; pl. 102, fig. 5; text-figs. 138P–R, X; 146H–J).

**Occurrence.**—As for material.

**Distribution.**—If the above comments are accepted, this species is recorded widely from the lower Cenomanian of South Africa, Madagascar, North Africa, England (?), Ukraine, Azerbaijan, and Japan.

#### Systematic allocation of *Hypoturrilites* in the Turrilitidae

When Dubourdieu (1953, p. 41, fig. 13) established the genus *Hypoturrilites*, he was not confident about its systematic position in the family Turrilitidae. He tentatively indicated it as one of the divergences from *Pseudhelicoceras* in parallel with *Mariella* [= "*Paraturrilites*" in his paper] and *Ostlingoceras*. At about the same time, but probably after the appearance of Dubourdieu's paper, *Mesoturrilites* was proposed by Breistroffer (1953, p. 1351). Its type species, *M. aumalensis* (Coquand, 1862), is somewhat similar to *Hypoturrilites* in having an upper row of fairly large tubercles at about the midflank and three rows of small tubercles in the lower part. In many species of *Hypoturrilites*, however, the large tubercles of the upper row at about the midflank are less numerous than the small ones in each of the lower three rows. In *M. aumalensis* and many other species of *Mesoturrilites* the small tubercles in each row are equal in

number to the large ones of the upper row. In morphological terms the typical species of *Mesoturrilites* can be regarded as a development of *Mariella* in which the ribbing was reduced and the tubercles in the lower rows are spirally elongated, as Wright and Kennedy (1996, p. 346) mentioned as one of the possible cases. In some other cases the ribbing remained in such ways as in *Mesoturrilites boerssomensis* (Schlüter, 1876), *M. serpuliforme* (Coquand, 1862) and *M. aff. corrugatus*. The latter subgroup of *Mesoturrilites* is fairly similar to *H. nodiferus* or to *H. tuberculatoplicatus*, in which, however, the midflank tubercles are enlarged and reduced in number.

The relationship of *Hypoturrilites* with *Mariella* takes a more definite shape. An actual morphological, if not phylogenetical, transition is observed between such a form of *Mariella* (*M.*) *bergeri* (Brongniart, 1822) as illustrated by Kennedy (1996, fig. 28p, o) from the uppermost part of the Albian and the typical form of *Hypoturrilites primus* Atabekian (1985, p. 60, pl. 16, fig. 1; pl. 17, fig. 1; Matsumoto, 2000, p. 6, fig. 2–3) from the lower Cenomanian.

*Hypoturrilites betaitraensis* Collignon, 1964 (p. 13, pl. 320, figs. 1387, 1388) (Wright and Kennedy, 1996, p. 375, pl. 102, fig. 12; text-fig. 134F–I), from the lower Cenomanian of Madagascar, South Africa, Algeria, West Europe and Turkmenistan, shows a pair of delicate ribs, of which one runs from the large tubercle upward to the interwhorl junction while the other is intercalatory between the large tubercles. Its small tubercles are conical or obliquely clavate as in many species of *Mariella*. The riblets similar to the above-mentioned delicate ribs are discernible and the small tubercles of the second and third rows are spirally elongated in *H. yabei*.

Although the details of the phylogenetical relations are practically unknown, it is interesting to note that *Mariella* extended from the Albian to the Cenomanian and that numerous species of *Hypoturrilites* and several species of *Mesoturrilites* evolved almost simultaneously in early Cenomanian time.

#### Conclusions

(1) In this paper *Hypoturrilites* is studied based on materials from the Ikushunbetsu Valley of the Mikasa district. As a result, *H. gravesianus* (d'Orbigny, 1842), *H. wrighti* sp. nov., *H. komotai* (Yabe, 1904), *H. yabei* Collignon, 1964, and *H. nodiferus* (Crick, 1907) are distinguished.

(2) In addition to the establishment of a new species, *H. wrighti*, the revised descriptions have made clear the distinction between *H. komotai* and *H. yabei*. *H. nodiferus* was proposed long ago on the basis of a fragmentary whorl but it is now well defined, showing its diagnosis, variation, and affinities with other species.

(3) Doubts about the occurrence of *H. komotai* are cleared up by ascribing its derivation to a lower Cenomanian bed. Thus, the number of described species from Hokkaido, including the recently reported *H. aff. mantelli* (Sharpe, 1857) and *H. primus* Atabekian, 1985 from the Shuparo area (Matsumoto, 2000), is altogether seven, about half of the described species from various regions of the world.

(4) The systematic allocation of *Hypoturrilites* in the family



Turritidae is discussed. As a conclusion, numerous species of *Hypoturritiles* seem to have evolved almost simultaneously from *Mariella* in the early Cenomanian age. At about the same time several species of *Mesoturritiles* may have evolved also from *Mariella*. A few atypical species of *Hypoturritiles* show a morphologically intermediate appearance between typical *Hypoturritiles* and *Mesoturritiles*.

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# Late Miocene ostracodes from the Kubota Formation, Higashi-Tanagura Group, Northeast Japan, and their implications for bottom environments

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**Abstract.** Sixty-seven ostracode species including those in open nomenclature are identified in thirty-six samples from the upper Miocene Kubota Formation, Higashi-Tanagura Group, distributed in Fukushima Prefecture, northeastern Japan. The lower part of the Kubota Formation yields *Spinileberis* sp. dominantly. In the middle to upper part of the formation, dominant species are *Schizocythere kishinouyei* (Kajiyama), *Kotoracythere abnorma* Ishizaki, *Hanaiborchella triangularis* (Hanai), *Cytheropteron miurense* Hanai, *Paracytheridea neolongicaudata* Ishizaki and *Finmarchinella japonica* (Ishizaki). Most of these species live off southwestern Japan under a subtropical to warm marine climate regime, but cryophilic and circumpolar species also occur sparsely in the middle to upper part. The ostracode assemblages indicate that the lower and the middle to upper parts of the Kubota Formation were deposited in an enclosed inner bay influenced by warm water and a warm shallow sea, respectively. Principal component analysis reveals that the influence of open sea water became strong in the upward sequence of the middle part. Analyses of ostracode faunas indicate that the Shiobara fauna from the Kubota Formation flourished in warm-water conditions.

**Key words:** Kubota Formation, Late Miocene, Ostracoda, Shiobara fauna

## Introduction

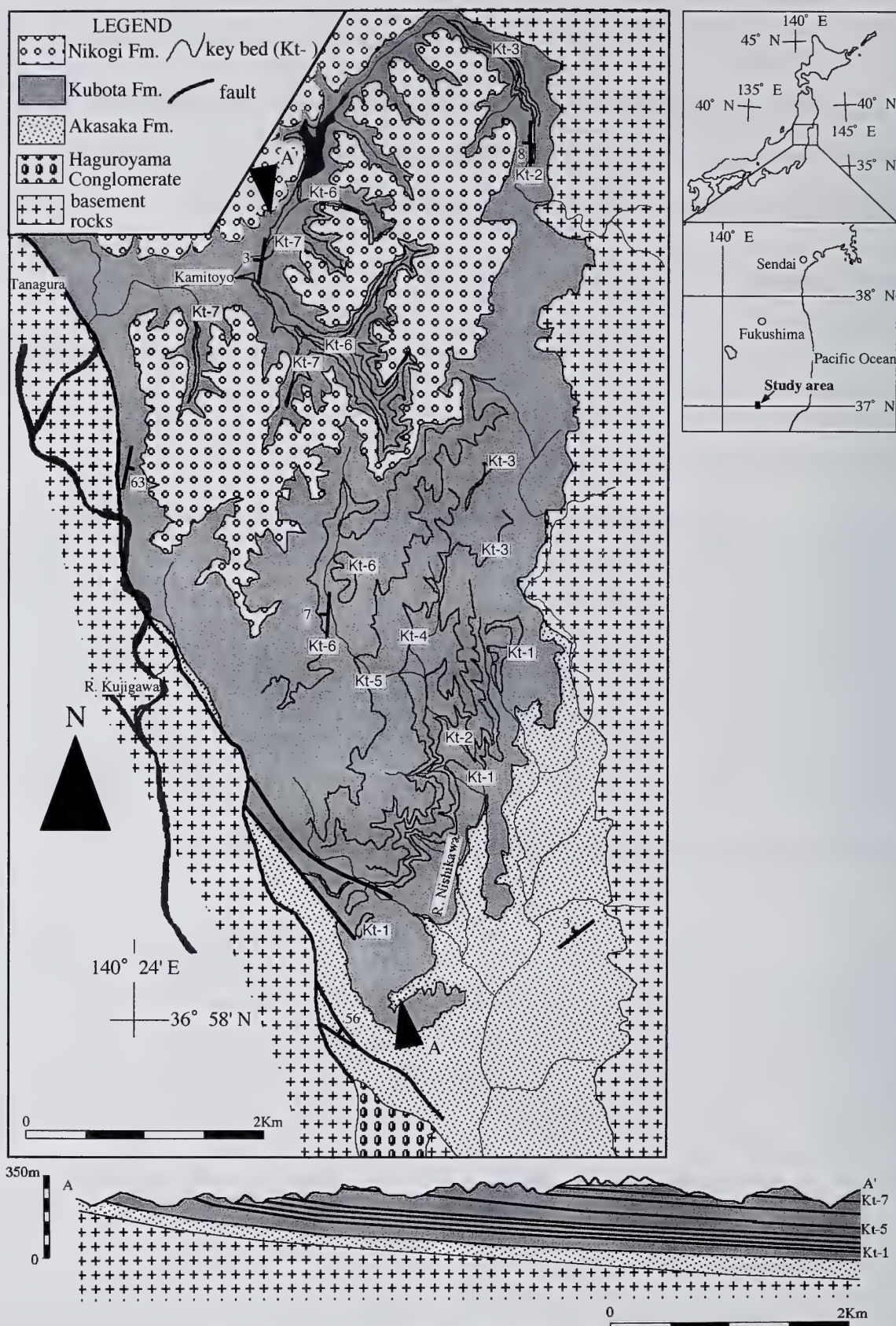
The Kubota Formation is known as one of the units containing the Shiobara fauna (Iwasaki, 1970), which flourished in Northeast Japan during the middle to late Miocene.

Chinzei and Iwasaki (1967) and Iwasaki (1970) considered that the Akasaka and Kubota Formations of the Higashi-Tanagura Group were deposited contemporaneously in an inner bay. Furthermore, these authors reconstructed a Higashi-Tanagura Bay on the basis of the lithology and geometry of the basin, discussing the paleoecology of the molluscan assemblages. In their discussion, Chinzei and Iwasaki (1967) compared the molluscan assemblages in the eastern Tanagura area with ones belonging to the Kadonosawa and Tatsunokuchi faunas, and recognized parallel communities. Iwasaki (1970) made a comparison with the molluscan assemblages in the eastern Tanagura, Shiobara, and Takasaki areas, where nearly contemporaneous deposits are distributed.

Consequently, he recognized parallel communities between them and defined the Shiobara-type fauna (Shiobara fauna).

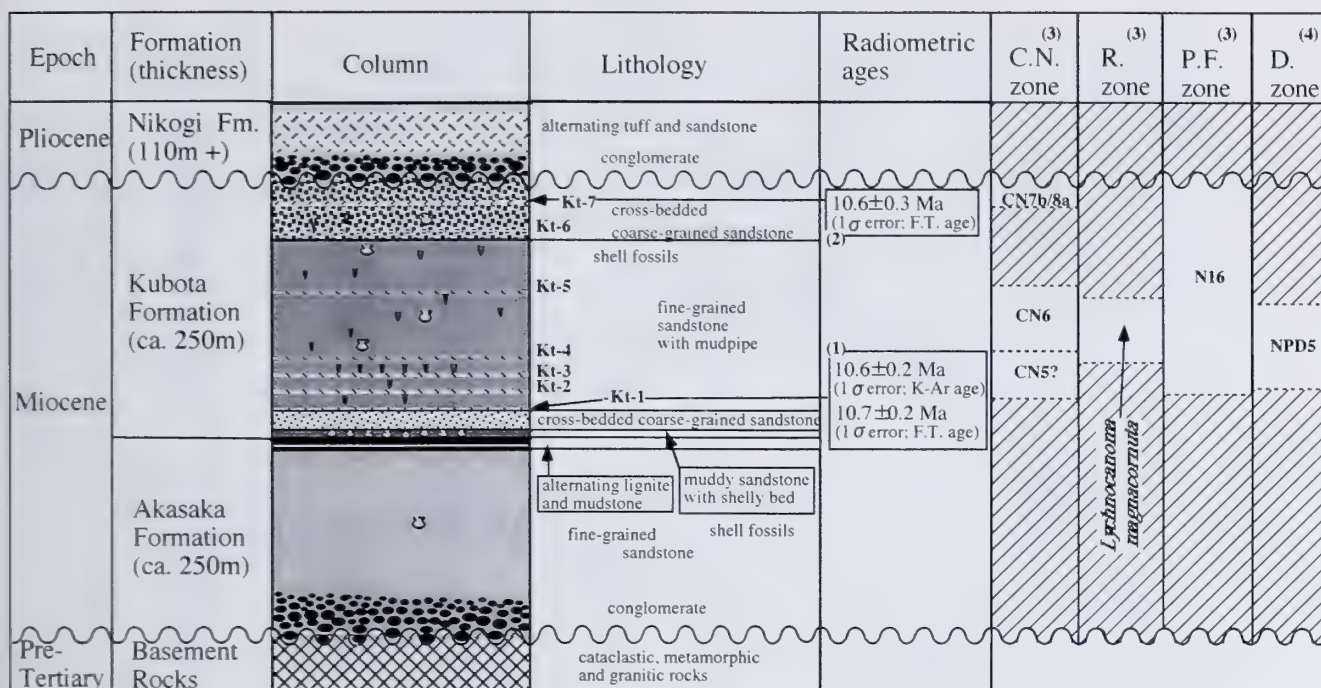
The Shiobara fauna was defined as a cold-water fauna which lived in inner bays or coastal areas (e.g. Chinzei, 1963; Chinzei and Iwasaki, 1967; Chinzei, 1986). Recently some workers, however, pointed out that the fauna flourished in warm- to mild-temperate realms rather than cold-temperate ones, or contained warm-water species as well as cold-water ones (e.g. Ogasawara *et al.*, 1985; Ogasawara, 1994; Ozawa *et al.*, 1996). Thus, the Shiobara fauna has been studied by many workers paleoecologically.

Many studies on the Miocene paleoenvironments have been made using molluscan fossils. For example, Chinzei (1986) and Ogasawara (1994) summarized the molluscan faunas of the late Cenozoic of Japan in the light of paleoclimates. Chinzei (1986) stated that Northeast Japan was influenced by cold water during the middle to late Miocene, since he regarded the Shiobara fauna as a cold-water fauna. On the other hand, Ogasawara (1994) thought



**Figure 1.** Geological sketch map and geological cross section of the eastern Tanagura area. Partly modified after Shimamoto *et al.* (1998) for the geological map.





(1) Takahashi *et al.* (2001) (2) Takahashi *et al.* (in press) (3) Shimamoto *et al.* (1998) (4) Yanagisawa *et al.* (2000)

**Figure 2.** Diagram showing the Neogene sequence in the eastern Tanagura area and biostratigraphy and radiometric ages of tuff layers of the Kubota Formation. Compiled after Shimamoto *et al.* (1998) and Yanagisawa *et al.* (2000) for biostratigraphy and Takahashi *et al.* (2001) and Takahashi *et al.* (in press) for radiometric ages.

that marine climates in Northeast Japan were warm- to mild-temperate during the middle to late Miocene, based on the modern distribution of molluscan genera and the marine zoogeographic divisions of Nishimura (1981). Paleoclimates suggested by molluscan fossils have been based on their biogeography and phylogeny. However, only a few studies have been made on other fossil groups from deposits yielding the Shiobara fauna.

To approach the problems mentioned above, we quantitatively examined ostracodes from the upper Miocene Kubota Formation of the Higashi-Tanagura Group.

### Geological setting

The eastern Tanagura area lies about 70 km south of Fukushima City, Fukushima Prefecture, northeastern Japan (Figure 1).

The geology of the eastern Tanagura area has been studied by many workers (e.g., Chinzei and Iwasaki, 1967; Iwasaki, 1970; Otsuki, 1975; Shimamoto *et al.*, 1998). The Miocene distributed in the eastern Tanagura area comprises two formations: the Akasaka and Kubota Formations (Figures 1, 2). The Kubota Formation overlies conformably the Akasaka Formation and is overlain unconformably by the Pliocene Nikogi Formation. On the basis of lithology, the Kubota Formation is divided into three parts (Shimamoto *et al.*, 1998): the lower part is composed of muddy fine-grained sandstone, yielding abundant molluscan fossils, and me-

dium- to coarse-grained sandstone; the middle part muddy fine-grained sandstone with mud-pipes and tuffaceous sandstone; the upper part cross-bedded coarse-grained sandstone. Many felsic tuff layers are intercalated in the middle to upper part, in which Shimamoto *et al.* (1998) recognized seven layers as keybeds (Kt-1 to Kt-7 tuff layers).

The geological age of the Kubota Formation has been determined by means of planktonic microfossils and radiometric dating of tuff layers (e.g., Aita, 1988; Takahashi and Amano, 1989; Taketani and Aita, 1991; Shimamoto *et al.*, 1998; Yanagisawa *et al.*, 2000; Takahashi *et al.*, 2001; Takahashi *et al.*, in press). Shimamoto *et al.* (1998) verified that the middle and upper parts of the Kubota Formation can be assigned to the calcareous nannofossil Zone CN6 to CN7/8a of Okada and Bukry (1980), planktonic foraminifer Zone N16 of Blow (1969) and the radiolarian *Lychnocanoma magnacornuta* Zone of Motoyama and Maruyama (1996). Yanagisawa *et al.* (2000) studied the diatom assemblages from the Kubota Formation for the first time and correlated the middle part with the diatom Zone NPD5C of Yanagisawa and Akiba (1998) (Figure 2).

On the other hand, Takahashi *et al.* (2001) dated the radiometric ages of a biotite-rich tuff layer, recognized as a keybed, the Kt-1 tuff layer, by Shimamoto *et al.* (1998). They reported the zircon fission-track age (F.T. age) and biotite potassium-argon age (K-Ar age) of the Kt-1 tuff layer to be  $10.7 \pm 0.2$  Ma (1  $\sigma$  error) and  $10.6 \pm 0.2$  Ma (1  $\sigma$  error). Moreover, Takahashi *et al.* (in press) dated the zircon fis-



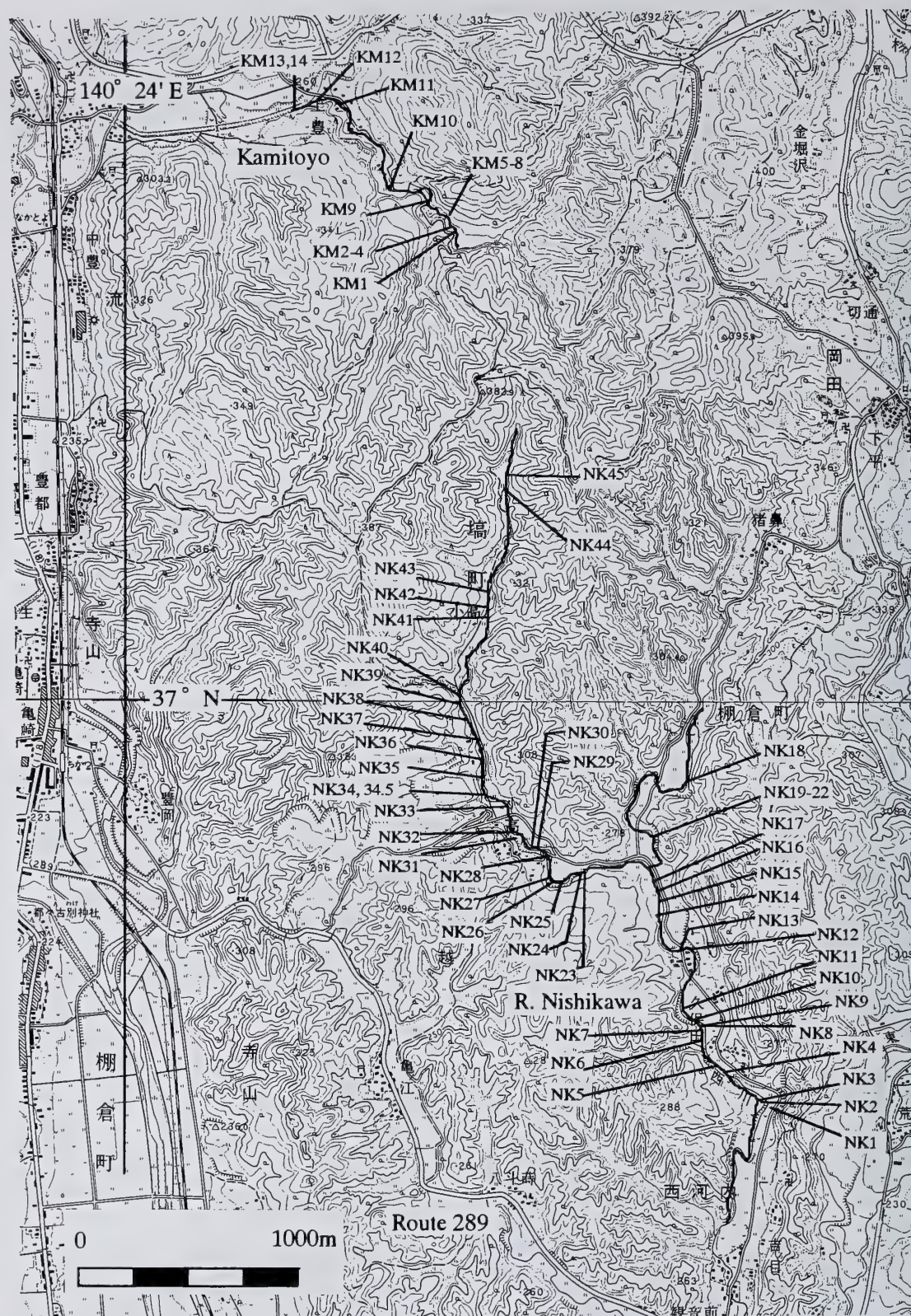
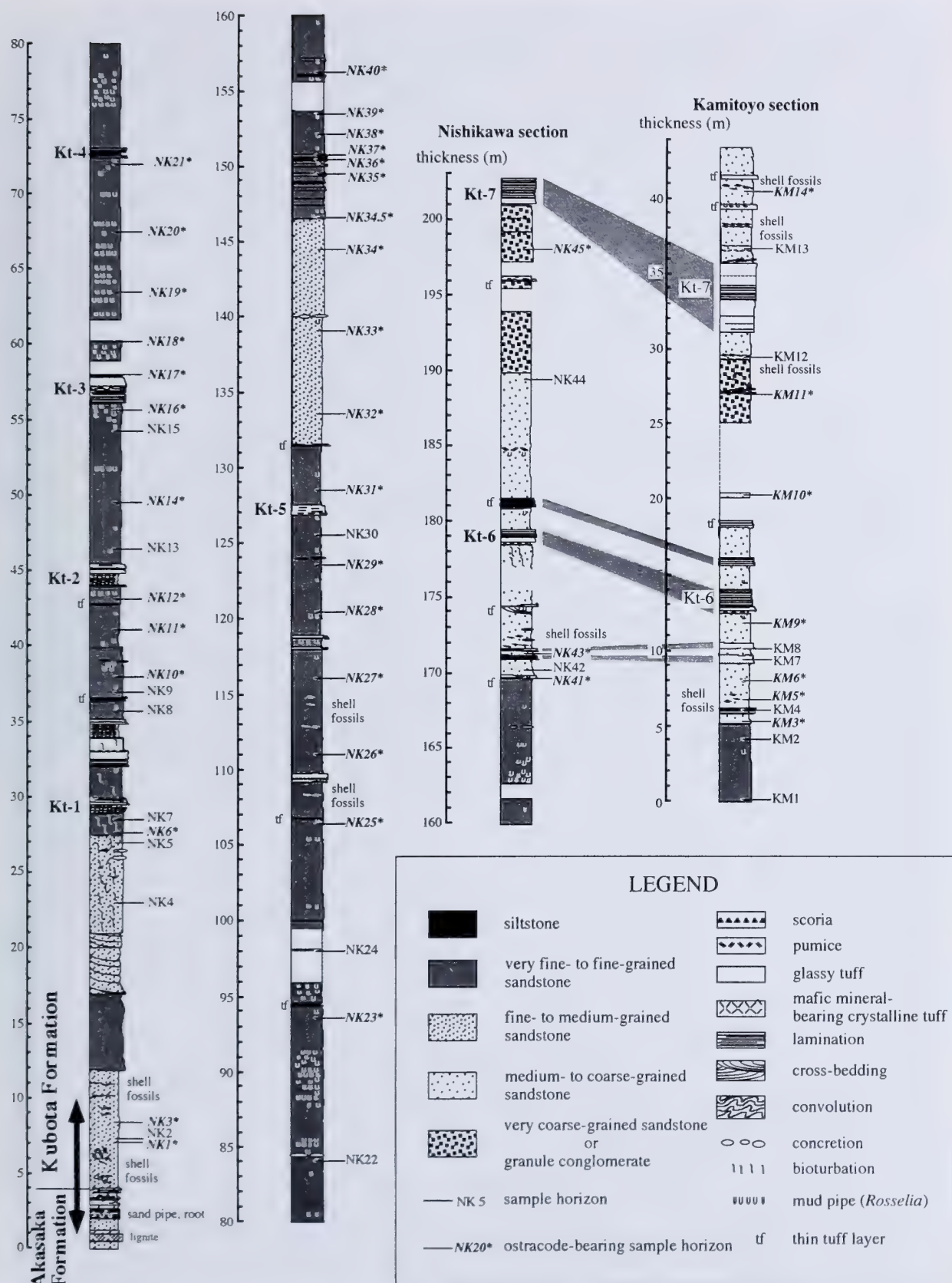


Figure 3. Map showing the ostracode fossil localities (a part of 1:25,000 map of "Tanagura" and "Hanawa" published by Geographical Survey Institute of Japan).





sion-track age of a felsic tuff, Kt-7, to be  $10.6 \pm 0.3$  Ma (1  $\sigma$  error) (Figure 2). These reported microfossil and radiometric ages do not contradict the biochronology of Saito (1999).

### Materials and methods

We collected 60 sediment samples from two sections of the Kubota Formation (Figures 3, 4) and examined 40 samples: 33 samples from the Nishikawa section and 7 samples from the Kamitoyo section. The Nishikawa section along the Nishikawa River is typical of the Kubota Formation (Shimamoto *et al.*, 1998). The upper part is better exposed in the Kamitoyo section along the Hokkawa River. We collected sediment samples from the Kamitoyo section to examine fossil ostracodes from the upper part of the Kubota Formation. These two sections are well correlated to each other by virtue of five keybeds.

Eighty grams of dried sediments were treated by using a saturated sodium sulfate solution and naphtha (Maiya and Inoue, 1973; Oda, 1978), washed through a 200 mesh sieve screen, and dried again. These procedures were repeated until the whole sediment sample became disintegrated. A fraction coarser than  $125\mu\text{m}$  (115 mesh) was sieved and divided by a sample splitter into aliquot parts, from which 100 to 200 individuals were picked with a fine brush under the binocular microscope. We took micrographs with a JEOL Field Emission Scanning Electron Microscope, JSM-6330F to identify the taxonomic relationships of the fossil ostracodes (Figures 5, 6). The results of our identifications are listed in Figure 7. In this figure, the estimated preservation of ostracodes in each sample is as follows: good means the sample contained abundant specimens easily identified to species level; poor, the sample contained mostly specimens identified with difficulty to species level; moderate indicates somewhere between good and poor.

We examined ostracode assemblages in detail from those samples, each represented by more than fifty individuals by means of the proportions (relative abundance) of major species, species diversity and equitability and performed principal component analysis on data for abundance of major forty species.

### Ostracode assemblages from the Kubota Formation

Ostracodes occurred in 36 samples and did not occur in 4 samples (samples NK1, 17, 18 and 45). We identified 67 ostracode taxa including those left in open nomenclature (Figure 7).

The ostracode assemblages from the Kubota Formation

can be distinctly divided into two groups (Figure 8). In the lower part of the formation, *Spinileberis* sp. accounts for more than 90% of the assemblage. The genus *Spinileberis* has been reported to occur abundantly on muddy bottoms in Recent enclosed inner bays (e.g. Hanai, 1961; Ikeya and Shiozaki, 1993).

In the middle to upper part, *Schizocythere kishinouyei* (Kajiyama), *Kotorocythere abnormalis* Ishizaki, *Hanaiborchella triangularis* (Hanai), *Cytheropteron miurense* Hanai, *Paracytheridea neolongicaudata* Ishizaki, *Finmarchinella japonica* (Ishizaki) and so on occurred. *S. kishinouyei* occurs most dominantly, forming 20 to 40% of the number of specimens in the assemblage. Subordinate are *K. abnormalis* and *H. triangularis*, accounting for 10 to 20% of the number of specimens in the assemblage. Other species represent less than 10%. Most species are reported to live in coastal areas and the open sea under the influence of the Kuroshio Warm Current (e.g. Hanai, 1957, 1970; Ishizaki, 1981; Zhou, 1995; Tsukawaki *et al.*, 1997, 1998). All of these species are known to represent the Shiobara fauna (Ishizaki, 1966; Irizuki and Matsubara, 1994, 1995; Ishizaki *et al.*, 1996; Irizuki *et al.*, 1998). Through the upper horizons of the middle part to the upper part, the relative abundance of *Kotorocythere abnormalis* increases (Figure 8).

### Faunal structures

The faunal structures of ostracode assemblages were expressed by the following four indices: species diversity [ $H(S)$ ], equitability ( $Eq.$ ), the number of species, and number of individuals per 10 g sediment sample. These indices have been used extensively in paleoecology. Figure 9 shows vertical changes of these indices. Changes in faunal structures may be related to environmental changes (e.g., Buzas and Hayek, 1998). Species diversity [ $H(S)$ ] and equitability ( $Eq.$ ) are expressed by the Shannon-Wiener formula and the equation of Buzas and Gibson (1969), respectively:

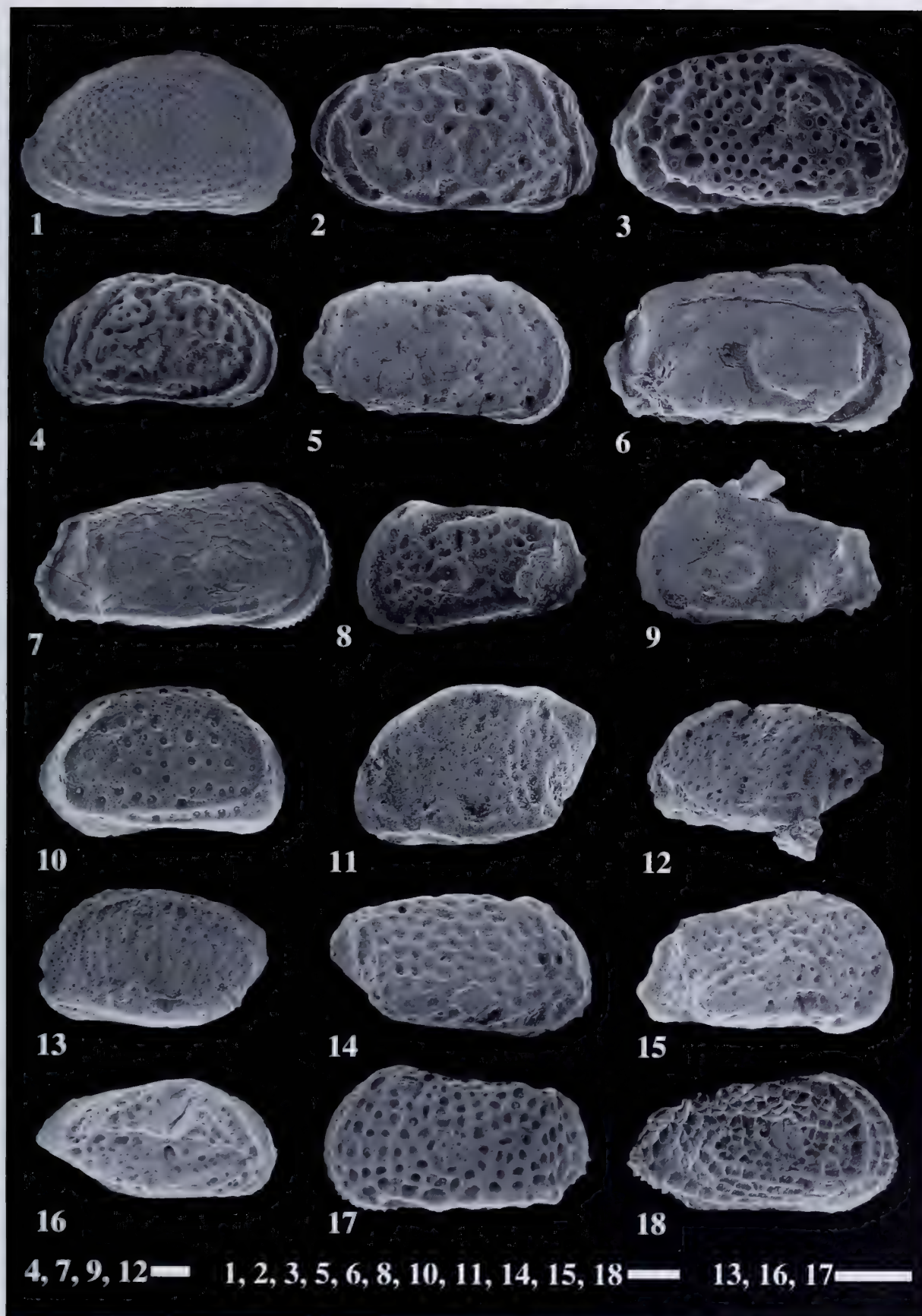
$$H(S) = -\sum p_i \ln p_i \text{ and } Eq. = \exp[H(S)]/S$$

where  $p_i$  means the proportion (relative abundance) of the  $i$ -th species in a sample and  $S$  the number of species.

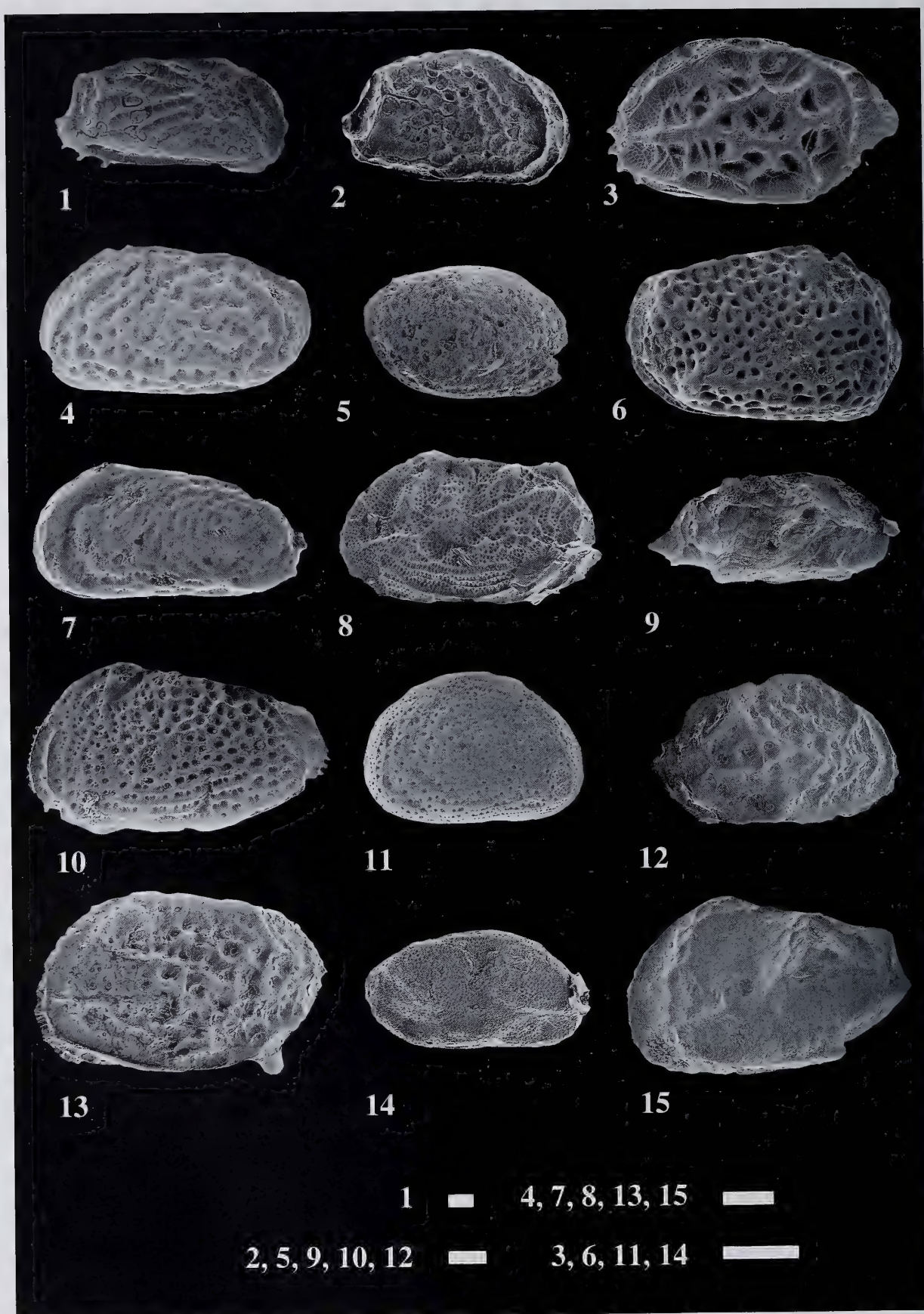
In the middle part of the Kubota Formation, the values of  $H(S)$  and  $Eq.$  range from 2.08 to 3.00 and from 0.44 to 0.64, respectively. The number of species in each sample varies from 20 to 40. Vertical changes of  $Eq.$  values are little.  $H(S)$  values and the number of species change synchronously. Through the upper horizon of the middle to upper part (samples NK41 and KM3),  $H(S)$  values and the number

→ **Figure 5.** Scanning electron micrographs of selected ostracode species from the Kubota Formation. All specimens, except for one juvenile one (7), represent adult valves. All scale bars indicate 100  $\mu\text{m}$ . RV = right valve; LV = left valve. 1: *Aurila* sp., RV, loc. NK27. 2: *Callistocythere hatatensis* Ishizaki, RV, loc. NK34.5. 3: *Callistocythere kotorai* Ishizaki, RV, loc. NK35. 4: *Callistocythere* sp.2, LV, loc. NK36. 5: *Coquimba* cf. *ishizakii* Yajima, RV, loc. NK25. 6: *Coquimba* sp.1, RV, loc. NK10. 7: *Coquimba* sp.2, RV, loc. NK27. 8: *Cornucoquimba saitoi* (Ishizaki), LV, loc. NK35. 9: *Cornucoquimba moniwiensis* (Ishizaki), LV, loc. NK21. 10: *Cythere ostenipponica* Hanai, RV, loc. NK27. 11: *Cytheropteron miurense* Hanai, LV, loc. KM3. 12: *Cytheropteron* cf. *sawanense* Hanai, LV, loc. NK10. 13: *Cytheropteron subuchioi* Zhao, LV, loc. NK27. 14: *Eucytherura neoalae* Ishizaki, RV, loc. NK21. 15: *Finmarchinella japonica* (Ishizaki), RV, loc. NK27. 16: *Hanaiborchella triangularis* (Hanai), RV, loc. NK27. 17: *Yezocythere gorokuensis* (Ishizaki), LV, loc. NK27. 18: *Trachyleberis* sp., RC, loc. NK35.



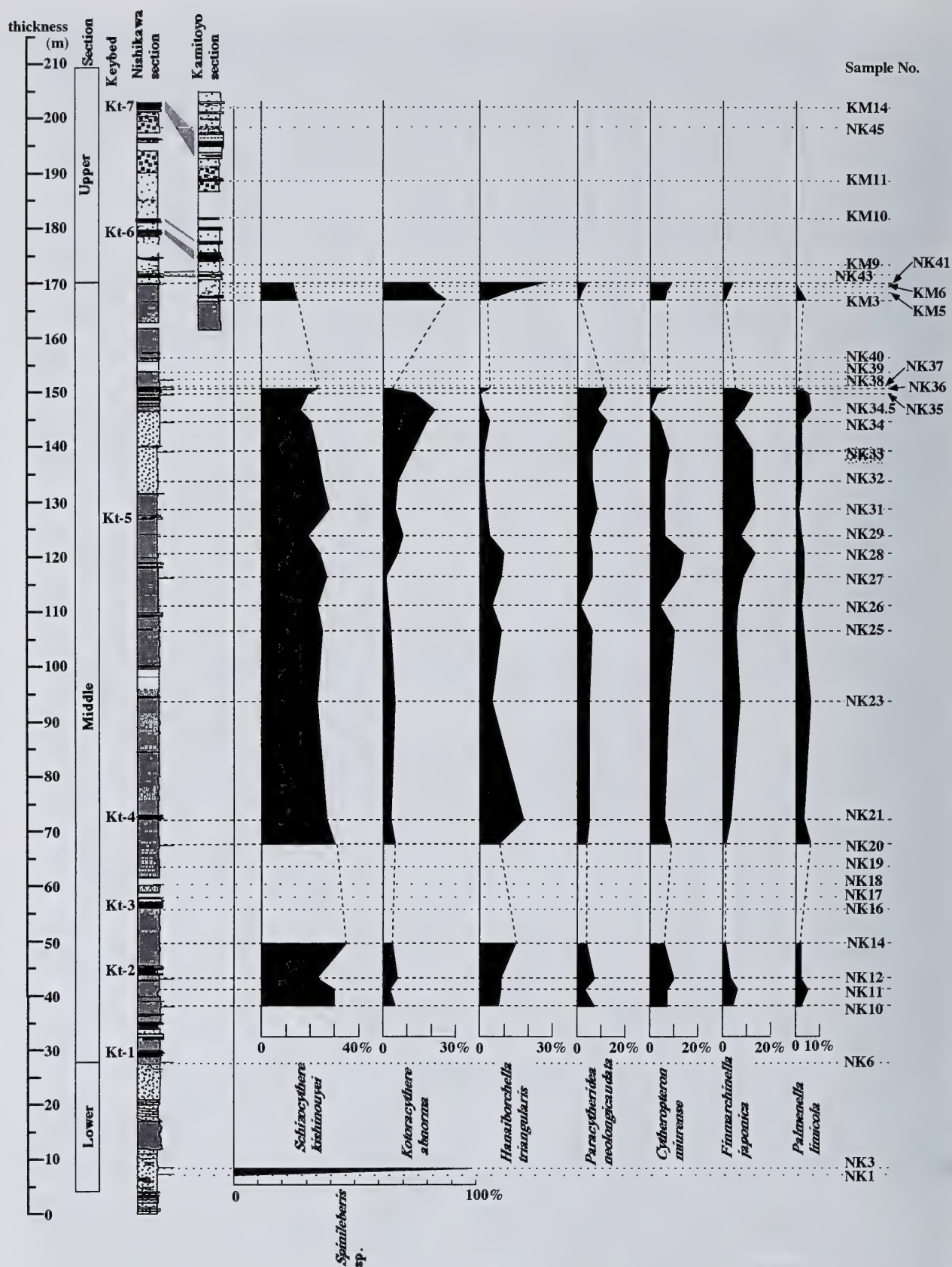








species/sample	NK3	NK6	NK10*	NK11*	NK12*	NK14*	NK16	NK19	NK20*	NK21*	NK23*	NK25*	NK26*	NK27*	NK28*	NK29*	NK31*	NK32*	NK33*	NK34*	NK34.5*	NK35*	NK36*	NK37	NK38	NK39	NK40	NK41*	NK43	NK48*	KM5	KM6	KM9	KM10	KM11	KM14			
<i>Acanthocythereis</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Aurilia cymba</i> (Brady)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
* <i>Aurilia</i> sp.	0	0	5	1	0	0	0	0	0	0	0	0	2	2	11	5	7	12	5	6	4	4	10	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* <i>Aurilia</i> spp.	1	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	2	0	0	3	3	0	3	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	
<i>Callistocythere katonai</i> Ishizaki	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	
* <i>Callistocythere hatatensis</i> Ishizaki	0	0	1	1	0	0	0	0	0	0	1	1	0	0	2	0	2	0	3	14	4	11	8	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
* <i>Callistocythere rugosaformis</i> Ishizaki	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0		
* <i>Callistocythere subaenensis</i> Ishizaki	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Callistocythere undulatifacialis</i> Hanai	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Callistocythere</i> sp.1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
* <i>Callistocythere</i> sp.2	0	0	3	1	0	0	0	0	0	0	0	2	0	3	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Callistocythere</i> spp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0		
* <i>Coquimba cf. ishizaki</i> Yajima	0	0	0	0	1	0	0	0	0	0	0	1	4	2	0	0	0	0	3	5	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
* <i>Coquimba</i> sp.1	0	0	1	2	0	0	0	0	0	1	4	5	12	3	0	13	14	12	10	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Coquimba</i> sp.2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Coquimba</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
* <i>Coquimba</i> ? spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
* <i>Cornucoquimba montensis</i> (Ishizaki)	0	0	5	7	8	5	0	0	5	4	12	0	4	4	2	8	7	2	10	1	0	3	5	0	0	0	0	0	0	1	0	1	0	0	0	0	1		
* <i>Cornucoquimba satoi</i> (Ishizaki) s.l.	0	0	8	9	2	1	0	0	6	7	14	16	4	13	14	6	5	4	0	7	19	9	7	0	0	0	0	0	1	4	14	9	1	0	5	0	2		
* <i>Cornucoquimba</i> spp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
* <i>Cythere omanipponica</i> Hanai	0	0	0	7	1	0	0	0	0	0	2	2	2	3	3	1	2	2	1	1	5	4	12	0	0	0	1	0	1	3	2	0	0	0	0	0	1		
* <i>Cythere</i> spp.	0	0	1	6	1	0	0	0	6	4	14	1	9	10	4	3	6	4	6	2	8	9	0	2	1	0	0	3	0	0	1	1	0	0	0	0	0		
* <i>Cythere</i> ? spp.	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
* <i>Cytheropteron murensense</i> Hanai	0	0	11	12	10	6	0	0	10	8	18	17	6	28	24	11	15	10	18	9	1	6	14	0	0	0	0	0	7	0	5	2	0	0	0	0	2		
* <i>Cytheropteron swanense</i> Hanai	0	0	2	2	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0		
<i>Cytheropteron cf. swanense</i> Hanai	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Cytheropteron subaenensis</i> Zhao	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
* <i>Cytheropteron uchii</i> Hanai	0	0	1	3	3	0	0	0	3	2	6	1	0	1	0	1	0	3	4	0	1	2	4	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	
<i>Cytheropteron</i> sp.1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Cytheropteron</i> spp.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0		
* <i>Euxithenura neolae</i> Ishizaki	0	0	4	4	3	1	0	0	0	3	2	1	2	0	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
* <i>Finmarthinella japonica</i> (Ishizaki) s.l.	0	0	7	10	3	1	0	0	1	4	16	8	10	19	22	14	33	22	26	9	17	24	7	0	0	0	0	7	3	0	1	0	0	0	1	0	0		
<i>Finmarthinella</i> sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0		
<i>Finmarthinella</i> spp.	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
* <i>Finmarthinella</i> ? spp.	0	0	0	0	3	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
* <i>Hanaiorhynchella triangularis</i> (Hanai)	0	1	13	16	9	14	1	2	8	23	11	15	8	22	17	7	7	4	5	8	5	1	7	2	2	1	2	20	1	3	0	0	0	0	0	1			
* <i>Hemicythere kitanipponica</i> Tabuki	0	0	2	3	0	0	0	0	1	0	3	0	10	0	0	4	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Hemicythere</i> spp.	0	0	0	1	0	0	0	0	2	0	1	1	1	1	0	2	1	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Hemicytherura clathrata</i> (Sars)	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0		
* <i>Hemicytherura cuneata</i> Hanai	0	0	0	1	0	0	0	0	0	0	0	0	1	0	3	2	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0		
* <i>Hemicytherura kajiyamai</i> Hanai	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
<i>Hemicytherura kamayuchi</i> (Tabuki)	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
* <i>Hermanites postero-costatus</i> Ishizaki	0	0	2	3	1	0	0	0	0	0	1	1	3	2	0	2	3	2	5	0	1	4	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0		
* <i>Kotoracythere abnormalis</i> Ishizaki	0	5	9	5	6	4	0	0	5	4	12	8	4	3	10	16	12	10	27	37	42	27	4	1	0	1	2	14	4	23	13	1	1	2	1	4			
* <i>Kotoracythere</i> spp.	0	0	0	0	0	0	0	0	0	0	6	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
* <i>Loxococoncha nozokiensis</i> Ishizaki	0	0	0	1	0	0	0	0	0	0	1	0	3	1	4	8	4	5	17	10	7	0	7	0	0	0	0	0	0	3	1	0	0	0	0	0	0		
* <i>Loxococoncha</i> spp.	0	0	0	0	9	7	0	0	0	1	0	0	0	0	0	0	7	0	0	0	1	0	1	0	0	0	0	1	0	0	3	0	0	0	0	0	0		
* <i>Loxocorniculum</i> sp.	0	0	3	6	0	0	1	0	6	0	3	0	4	0	0	11	1	4	4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0		
* <i>Melasteneropteron</i> sp.	0	0	0																																				





of species decrease.

The number of individuals in sample NK3 is 0.2 per 10 g sediment. Samples from the middle and upper parts contain about 40 to 400 and less than about 10 individuals per 10g, respectively.

### Principal component analysis

In order to elucidate bottom environments of the Kubota Formation, 21 samples which contained more than 50 individuals and 40 species represented by more than three individuals at least in a sample were subjected to Q-mode principal component analysis. The analysis was carried out to obtain clues to the intersample relationship and to identify end members (samples having extreme properties). However, the correlation coefficient may be considered inappropriate as a measure of similarity between samples because it requires calculation of variance across variables (Davis, 1986). Therefore, the analysis in this study was based on the covariance matrix. The computer program used in this study was a modified version written by Furuya and Obata (1996). The results of the analysis show that the first two components account for about 85 % of the total variation, which should be sufficient for discussion of general distribution patterns of the ostracode assemblages (Table 1). Figure 10 shows the stratigraphic distribution of eigenvectors in relation to the first two components.

#### The first component

This component explains more than 77% of the total variation. *Schizocythere kishinouyei* (score = +113.9), *Kotoracythere abnormalis* (score = +35.9), *Hanaiborchella triangularis* (score = +34.5) and *Cytheropteron miurense* (score = +32.6) contribute greatly to this component. They are abundant in most of the samples examined. Recent representatives of these species are mostly known to occur predominantly in littoral to sublittoral habitats, which are influenced by the Kuroshio Warm Current (e.g. Hanai, 1957, 1970; Ishizaki, 1966, 1981; Zhou, 1995; Tsukawaki *et al.*, 1997, 1998). The first component is interpreted to represent the abundance of ostracode species.

#### The second component

This component explains more than 7% of the total variation. *Kotoracythere abnormalis* (score = +32.0) and *Cornu-coquimba saitoi* s.l. (score = +8.8) have high positive scores of the second component. *Hanaiborchella triangularis* (score = -8.1), *Rotundracylethere?* sp. (score = -7.9) and *Schizocythere kishinouyei* (score = -7.1) have high negative scores of the second component. *K. abnormalis* and *C. saitoi* are extinct species. *K. abnormalis* occurs in the middle Miocene Hatatate Formation, but does not occur in the Moniwa Formation, which is overlain conformably by the Hatatate Formation (Ishizaki, 1966). Kitamura *et al.* (1986) suggested that the Hatatate and Moniwa Formations were

deposited in lower sublittoral to bathyal and upper sublittoral settings, respectively, based on sedimentary facies and benthic foraminifer assemblages. Hence, *K. abnormalis* is considered as having lived in the lower sublittoral zone under the influence of open sea water. Because *C. saitoi* also occurs in the Hatatate Formation, it is regarded as having lived under the influence of open sea water (Ishizaki, 1966). Thus, species having high positive scores are considered as having lived in the open sea. On the other hand, species having high negative scores are reported from Recent seas, except for *Rotundracylethere?* sp. *H. triangularis* is reported from the mouth of Ise and Mikawa Bays (Bodergat and Ikeya, 1988). *Rotundracylethere?* sp. occurs in the Pleistocene Sasaoka Formation (Ishizaki and Matoba, 1985). Because *Rotundracylethere?* sp. occurs with shallow marine molluscs, it is regarded as having likewise lived in shallow marine waters. *S. kishinouyei* is reported from an upper sublittoral zone under the influence of coastal currents in the eastern China sea (Ishizaki, 1981). Therefore, species having high negative scores are considered as having lived in shallow seas influenced by coastal currents. Consequently, the second component is interpreted as signalling changes of water mass: positive and negative eigenvectors represent the stronger and weaker influence of open sea water, respectively.

### Discussion

#### Water depths

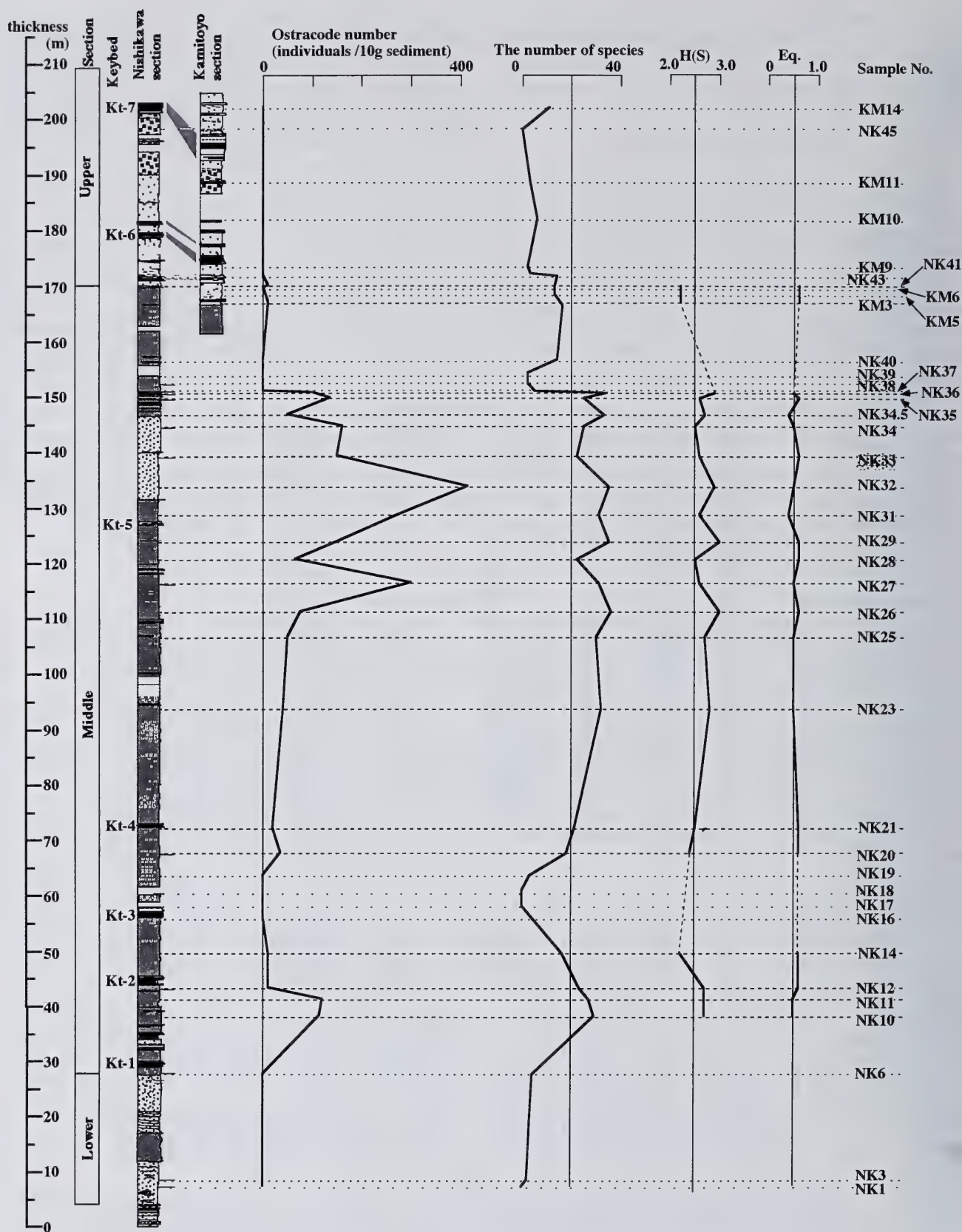
In the lower part of the Kubota Formation, *Spinileberis* sp. occurs dominantly. This fact suggests that the lower part was a deposit in an enclosed inner bay (e.g. Ikeya and Shiozaki, 1993).

Most of the ostracode species from the middle part of the formation are reported in Recent shallow seas, as mentioned above. Moreover, the faunal structures of the ostracode assemblages from the unit indicate high values of  $H(S)$ ,  $Eq.$  and the number of species. For example, the faunal structures of ostracode assemblages in the outer part of Uranouchi Bay show values of  $H(S)$ ,  $Eq.$  and the number of species that are 2.0 to 3.0, 0.4 to 0.6 and 20 to 40, respectively (Ishizaki, 1979). These values approximate those of the middle part. Thus, the ostracode assemblage from the middle part of the Kubota Formation represents a sublittoral setting. Vertical changes of the second component eigenvectors indicate that the influence of open sea water became stronger in the upward sequence.

In the upper part, the low occurrence of ostracodes means that paleodepths cannot be assessed, except for the horizon of the sample KM3. The sample KM3 has a positive second-component eigenvector and the horizon of the sample was deposited under the influence of open sea water.

As already mentioned, Iwasaki (1970) studied the molluscan fauna from the Kubota Formation. He reported

← **Figure 8.** Diagram showing the vertical changes for the relative abundance of major species. Broken lines show samples containing more than 50 individuals of ostracodes. Dotted lines represent samples containing less than 50 individuals. Loose dotted lines represent samples containing no ostracode. For explanation of columnar sections see the legend of Figure 4.





the *Ostrea* and *Anadara-Dosinia* assemblages from the lower part, the *Lucinoma-Turritella* assemblage from the middle part and the *Mizuhopecten-Chlamys* assemblage from the upper part. These molluscan assemblages represent the following habitat conditions, referring to the paleobathymetric indices of molluscan fossils shown by Ogasawara and Masuda (1989): 1) the lower part represents an inner-bay environment with water depths shallower than 30 m; 2) the middle part represents depths between 100 and 200 m; 3) the upper part represents depths of 30 m or less under the influence of the open sea. These estimates based on molluscan fossils from the Kubota Formation are generally consistent with the water depths suggested by ostracodes.

Shimamoto *et al.* (1998) examined foraminifer, radiolarian and molluscan fossils and showed the successive changes of the planktonic/benthic foraminifer ratio (P/B ratio). They thought that the lower part was deposited in an inner bay because of the occurrence of *Ostrea* of *in-situ* origin, while the middle part was in an open sea shallower than about 100 m based on P/B ratios. Consequently, they concluded that the Kubota Formation represents a sequence of marine transgression and regression. Vertical changes of water depths suggested by ostracodes are largely consistent with their views. On the other hand, decreasing frequency of radiolarians in the upward sequence of the middle part suggests that influence of the open sea water became feeble. This representation contradicts one based on vertical changes of second-component eigenvectors. Some workers have pointed out that radiolarian assemblages from the Kubota Formation contain many reworked individuals (Taketani and Aita, 1991; Shimamoto *et al.*, 1998). Therefore, the reported frequency of radiolarians is regarded as not sufficiently representing paleoenvironmental settings during deposition of the middle part. Consequently, the middle part was subject to the strong influence of open sea water in its upward sequence.

#### Marine climates

In the lower part of the Kubota Formation, the only dominant species is *Spinileberis* sp. Recent species of this genus are widely distributed from southern China to northern Japan and occur abundantly in bays influenced by warm coastal waters (e.g. Hanai, 1961; Ishizaki, 1971; Ikeya and Shiozaki, 1993). Hence, the lower part is considered to have been deposited under the influence of warm coastal waters.

In the middle part, Recent representatives of *Schizocythere kishinouyei*, *Hanaiborchella triangularis* and *Cytheropteron miurensis* among the dominant species are reported from shallow seas under the influence of the Kuroshio Warm Current (e.g. Ishizaki, 1981; Zhou, 1995). However, such circumpolar and cryophilic species as *Hemicytherura clathrata*, *Munseyella hatatensis*,

*Palmenella limicola*, *Finmarchinella japonica* s.l. and *Hemicythere kitanipponica* also occurred sparsely (Figure 10). Circumpolar and cryophilic species are members of high-latitude genera (Cronin and Ikeya, 1987). Irizuki and Matsubara (1995) and Irizuki *et al.* (1998) also reported that circumpolar and cryophilic species occurred with warm-water species in the Miocene deposits. They considered that the Miocene circumpolar and cryophilic species may not have experienced such subfrigid to frigid environments as their Recent counterparts and lived in slightly colder conditions than the other species because of the absence of fossil records for them from the mid-Neogene climatic optimum horizon of southwestern Japan (Ishizaki, 1963; Yajima, 1988, 1992). Hence, the middle part of the formation was deposited in a warm shallow sea under the feeble influence of cooler currents.

Ostracodes are sparse in the upper part of the formation. However, species forming assemblages do not show any distinct change, comparing with the assemblages from the middle part. Hence, the upper part may also have been deposited in warm-water conditions.

As mentioned above, Ogasawara (1994) studied the relations between marine climates and Neogene molluscan faunas, considering their tolerance for marine climates. Moreover, he divided the Shiobara fauna into older and younger faunas based on characteristic species of each fauna. The molluscan fauna from the Kubota Formation belongs to the younger Shiobara fauna, because *Mizuhopecten paraplebejus* and *Kaneharaia kaneharai*, both of which characterize the younger fauna, were reported (Iwasaki, 1970). Ogasawara (1994) mentioned that the younger Shiobara fauna had lived in the warm- to mild-temperate realms of Nishimura's (1981) zoogeographical classification of modern marine faunas around the Japanese Islands.

Marine paleoclimates represented by ostracode fauna from the Kubota Formation strongly supported Ogasawara's (1994) views.

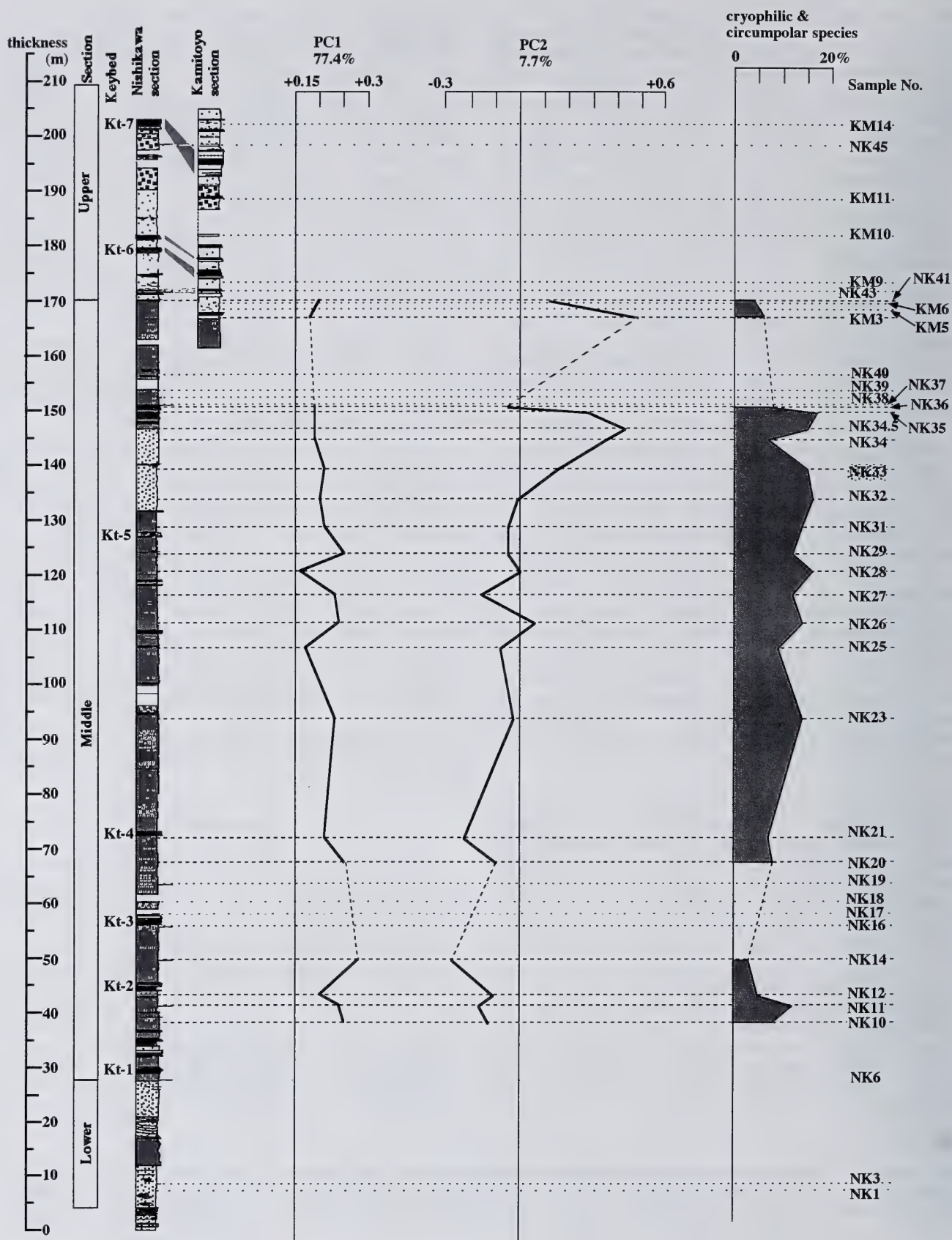
#### Conclusions

1) Sixty-seven ostracode species including those left in open nomenclature were reported for the first time from the upper Miocene Kubota Formation. The fauna is characterized by the abundance of warm-water species.

2) The ostracode fauna from the Kubota Formation reveals an enclosed inner bay paleoenvironment influenced by warm water for the lower part and a warm shallow sea under the feeble influence of cold water for the middle to upper part. Hence, the Shiobara fauna from the Kubota Formation flourished in a warm shallow sea.

3) Results of principal component analysis of successively collected ostracode samples suggest that the middle part of the Kubota Formation was strongly influenced by

← **Figure 9.** Diagram showing the vertical changes of the ostracode abundance of individuals per 10g sediment, number of species, species diversity ( $H(S)$ ) and equitability ( $Eq.$ ). Broken lines show samples containing more than 50 individuals of ostracodes. Dotted lines represent samples containing less than 50 individuals. Loose dotted lines represent samples containing no ostracode. For explanation of columnar sections see the legend of Figure 4.





**Table 1.** Summary of principal component analysis.

	Eigenvalue	Percentage	Cumulative Percentage
PC 1	380.5	77.4	77.4
PC 2	37.8	7.7	85.1

open sea water in its upward sequence.

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← **Figure 10.** Diagram showing vertical changes of eigenvectors with respect to the first two components and the proportion of cryophilic and circumpolar ostracode species. Broken lines show samples containing more than 50 individuals of ostracodes. Dotted lines represent samples containing less than 50 individuals. Loose dotted lines represent samples containing no ostracode. For explanation of columnar sections see the legend of Figure 4.



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# The systematic status of the genus *Miosesarma* Karasawa, 1989 with a phylogenetic analysis within the family Grapsidae and a review of fossil records (Crustacea: Decapoda: Brachyura)

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**Abstract.** The genus *Miosesarma* Karasawa (Decapoda: Brachyura: Grapsidae) known from the Miocene of Japan is redefined. A phylogenetic analysis of 22 genera of the family Grapsidae MacLeay is provided based on 41 adult morphological characters. A single tree is produced (length = 85, CI = 0.565, RI = 0.807, RC = 0.456). The analysis supports the monophyly of the subfamilies Plagusiinae Dana, Grapsinae MacLeay and Varuninae H. Milne Edwards. The analysis suggests that the Sesarminae Dana is polyphyletic and that *Cyclograpsus* H. Milne Edwards, *Helice* De Haan, *Metaplax* H. Milne Edwards and *Miosesarma* are derived as sister taxa to varunines. The tribe Cyclograpscaea H. Milne Edwards is treated as a subfamily Cyclograpsinae (*nomen. transl.*) consisting of *Cyclograpsus* (type genus), *Helice*, *Heterograpsus* Campbell and Griffin, *Metaplax*, *Miosesarma* and *Paragrapsus* H. Milne Edwards, which were previously placed within the Sesarminae. Within the Grapsidae, the Varuninae and Cyclograpsinae are sister groups nested as the most derived clade, followed by the Sesarminae, Grapsinae, and the most basal Plagusiinae. Five subfamilies within the Grapsidae are redefined based on the phylogenetic analysis. During a review of fossil records of the Grapsidae, 25 species, 17 genera and four subfamilies are recognized as fossils. *Maingrapsus* Tessier *et al.*, *Palaeograpsus* Bittner, and *Telphusograpsus* Lörenthey, known from the European Eocene, are referred to the family Goneplacidae H. Milne Edwards and *Sculptoplax* Müller and Collins from the Eocene of Hungary is referred to the Xanthidae MacLeay. Fossil grapsids exhibiting the dorsal carapace only can not confidently be referred to subfamilies.

**Key words:** Brachyura, Crustacea, Decapoda, Grapsidae, Phylogeny

## Introduction

The genus *Miosesarma* Karasawa, 1989 is an endemic genus known from the lower-middle Miocene of Japan (Karasawa, 1989, 1999; Kato, 1996). Karasawa (1989) originally placed the genus within the subfamily Sesarminae Dana, 1851 (Decapoda: Brachyura: Grapsidae) and demonstrated its close resemblance to extant sesarmines, *Helice* De Haan, 1835 and *Metaplax* H. Milne Edwards, 1852. Pereyra Lago (1993) and Schubart and Cuesta (1998) indicated that larval characters of *Helice* were similar to those of the grapsid subfamily Varuninae H. Milne Edwards, 1853. Schubart *et al.* (2000) suggested reclassification and phylogeny of the Grapsidae based upon molecular data, and that *Helice* and *Metaplax* should be classified within Varuninae.

The purpose of the present paper is to redefine the genus *Miosesarma* based on newly obtained specimens and to provide an adult morphology-based phylogenetic analysis for 22 genera of the Grapsidae. A review of fossil records of the Grapsidae is included.

## Phylogenetic analysis of the family Grapsidae MacLeay, 1838

### Materials and methods

A total of 25 species were examined with representatives from 22 genera including one extinct genus, *Miosesarma*, within the Grapsidae. Among these, extant species were collected from Japan, Thailand and Malaysia. The analyses were based on the examination of material deposited in the Mizunami Fossil Museum, Mizunami, Japan and the

Table 1. Taxa included in the analysis.

Family Grapsidae MacLeay, 1838	Genus <i>Sesarmops</i> Sèrene and Soh, 1970
Subfamily Grapsinae MacLeay, 1838	<i>Sesarmops intermedium</i> (De Haan, 1835)
Genus <i>Geograpsus</i> Stimpson, 1858	Subfamily Varuninae H. Milne Edwards, 1853
<i>Geograpsus grayi</i> (H. Milne Edwards, 1853)	Genus <i>Acmaeopleura</i> Stimpson, 1858
Genus <i>Grapsus</i> Lamarck, 1801	<i>Acmaeopleura parvula</i> Stimpson, 1858
<i>Grapsus albolineatus</i> Lamarck, 1818	Genus <i>Eriocheir</i> De Haan, 1835
<i>Grapsus tenuicrustatus</i> (Herbst, 1783)	<i>Eriocheir japonica</i> (De Haan, 1835)
Genus <i>Metopograpsus</i> H. Milne Edwards, 1853	Genus <i>Gaetice</i> Gistel, 1848
<i>Metopograpsus thukuhar</i> (Owen, 1839)	<i>Gaetice depressus</i> (De Haan, 1833)
Genus <i>Pachygrapsus</i> Randall, 1840	Genus <i>Hemigrapsus</i> Dana, 1851
<i>Pachygrapsus minutus</i> A. Milne Edwards, 1873	<i>Hemigrapsus sanguinensis</i> (De Haan, 1835)
Genus <i>Planes</i> Bowdich, 1825	Genus <i>Pseudograpsus</i> H. Milne Edwards, 1837
<i>Planes cyaneus</i> Dana, 1851	<i>Pseudograpsus</i> sp.
Subfamily Sesarminae Dana, 1851	Genus <i>Ptychognathus</i> Stimpson, 1858
Genus <i>Chasmagnathus</i> De Haan, 1833	<i>Ptychognathus</i> sp. aff. <i>P. ishii</i> Sakai, 1939
<i>Chasmagnathus convexus</i> De Haan, 1833	Genus <i>Varuna</i> H. Milne Edwards, 1830
Genus <i>Cyclograpsus</i> H. Milne Edwards, 1837	<i>Varuna litterata</i> (Fabricius, 1798)
<i>Cyclograpsus intermedius</i> Ortmann, 1894	Subfamily Plagusiinae Dana, 1851
Genus <i>Helice</i> de Haan, 1835	Genus <i>Percnon</i> Gistel, 1848
<i>Helice leachi</i> Hess, 1865	<i>Percnon planissimum</i> (Herbst, 1804)
Genus <i>Metaplex</i> H. Milne Edwards, 1852	Genus <i>Plagusia</i> Latreille, 1804
<i>Metaplex crenulata</i> (Gerstecker, 1856)	<i>Plagusia dentipes</i> De Haan, 1833
Genus <i>Miosesarma</i> Karasawa, 1989	
<i>Miosesarma japonicum</i> Karasawa, 1989	Family Xanthidae MacLeay, 1838
<i>Miosesarma naguraense</i> Kato, 1996	Genus <i>Leptodius</i> A. Milne Edwards, 1873
Genus <i>Nanosesarma</i> Tweedie, 1950	<i>Leptodius nudipes</i> (Dana, 1852)
<i>Nanosesarma minutum</i> (De Man, 1887)	Family Cancridae Latreille, 1803
Genus <i>Sesarma</i> Say, 1817	Genus <i>Cancer</i> Linnaeus, 1758
<i>Sesarma (Perisesarma) bidens</i> (De Haan, 1835)	<i>Cancer amphioetus</i> Rathbun, 1898
<i>Sesarma (Parasesarma) pictum</i> (De Haan, 1835)	

Natural History Museum and Institute, Chiba, Japan. The material examined is listed in Table 1. The subfamilial arrangement of the genera conforms to Sakai (1976), Manning and Holthuis (1981) and Karasawa (1989). Outgroups included two heterotrematous crabs, *Cancer amphioetus* Rathbun, 1898 (Cancridae) and *Leptodius nudipes* (Dana, 1852) (Xanthidae) outside of the Grapsidae (Table 1). Table 2 lists 41 adult morphological characters and character states used in the analysis. The missing data were scored unknown. The data matrix is provided in Table 3.

The phylogenetic analysis used PAUP version 3.1.1 (Swofford, 1993), utilizing a data matrix originating in MacClade version 3 (Maddison and Maddison, 1992). Heuristic search analyses were performed with the following options in effect: addition sequence, simple; one tree held at each step during stepwise addition; tree-bisection-reconnection (TBR) branch stepping performed; MULPARS option activated; steepest descent option not in effect; branches having maximum length zero collapsed to yield polytomies; topological constraints not enforced; tree unrooted; multistate taxa interpreted as uncertain; character state optimization, accelerated transformation (ACCTRAN). All characters were unordered, unscaled and equally

weighted.

### Characters

Forty-one characters were included in the data matrix (Table 3). There are 34 binary characters and 7 multistate characters. In the text, characters and character states are indicated by numbers in parentheses (e.g. 1-0 = character 1+character state 0).

**Carapace.**—In examined material the carapace is usually smooth (3-0; Figures 1.1, 1.2, 1.5-1.8, 4.11, 4.12, 4.15); however, all grapsine genera and a sesarmine *Sesarma* bear oblique ridges dorsally (3-1; Figure 1.3, 1.4). One outgroup taxon, *Cancer*, and two plagusiines, *Plagusia* and *Percnon*, possess frontal teeth (4-0; Figure 1.1, 1.2), while all other examined taxa have a straight frontal margin without teeth (4-1; Figure 1.3-1.8). Most taxa have a narrow orbital margin (5-0; Figure 1.1-1.4, 1.6), but a varunine *Hemigrapsus* and three sesarmines, *Chasmagnathus*, *Metaplex* and *Miosesarma*, possess wide orbital margins (5-1; Figures 1.5, 1.7, 1.8, 4.5, 4.11, 4.12, 4.15). Both outgroup taxa, all plagusiines and all grapsines lack infraorbital ridges (6-0; Figure 2.9-2.11); however, all sesarmines and all varunines bear infraorbital ridges (6-1;



**Table 2.** Characters and states used in the phylogenetic analysis.

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<b>Carapace</b>	
1	Ratio of carapace length/width: wider than long (0); about equal (1); long (2)
2	Maximum carapace width: midlength (0); anterior (1); posterior (2)
3	Carapace with oblique ridges dorsally: absent (0); present (1)
4	Frontal margin with frontal teeth: present (0); absent (1)
5	Orbital width: narrow (0); wide (1)
6	Infraorbital ridge: absent (0); present (1)
7	Upper orbital margin with notch: present (0); absent (1)
8	Lateral teeth: present (0); absent (1)
9	Pterygostomian and ventrolateral surfaces with oblique striae: absent (0); present (1)
<b>Eye stalk and antennule</b>	
10	Eye stalk: short (0); long (1)
11	Antennule: not visible dorsally (0); visible dorsally (1)
<b>Maxilliped 3</b>	
12	Ratio of merus/ischium: short (0); subequal (1); very short (2)
13	Anterolateral margin of merus: quadrate (0); expanded (1); convex (2)
14	merus and ischium with oblique, hairy ridge: absent (0); present (1)
15	Maxilliped 3 with wide rhomboidal gap: absent (0); present (1)
16	Exopod: wide (0); narrow (1)
17	Articulation of palp: anteromesial angle of merus (0); anterior margin of merus (1)
18	Dactylus: long (0); short (1)
<b>Abdomen</b>	
19	Male abdomen: fused somites (0); 7 somites (1)
20	Male abdomen width: narrow (0); wide (1)
<b>Thoracic sternum</b>	
21	Thoracic sternum width: narrow (0); wide (1)
22	Sternites 1 and 2: distinct (0); indistinct (1)
23	Suture between sternites 3 and 4: distinct (0); indistinct (1)
24	Median groove on sternite 3: present (0); absent (1)
25	Median groove on sternite 4: present (0); absent (1)
26	Button: present (0); absent (1)
27	Anterior end of sterno-abdominal cavity: shallow (0); sternite 4 (1); sternite 3 (2)
28	Cristiform margin of anterior sterno-abdominal cavity: absent (0); present (1)
29	Deeply concave lateral margin of sternites 3-4: absent (0); present (1)
30	Transverse groove on sternite 8: absent (0); present (1)
31	Sternite 8 visible in ventral view: indistinct (0); distinct (1)
32	Sternite 8 visible in posterior view: indistinct (0); distinct (1)
33	Location of male gonopore: coxae (0); sternite 8 (1)
34	Location of male gonopore on sternite 8: excluded (0); lateral (1); inner (2)
<b>Gonopod</b>	
35	Gonopods 1: sinuous (0); twist (1); linear (2)
<b>Pereiopods</b>	
36	Cheliped with elongate, slender palm: absent (0); present (1)
37	Chelipeds with pectinated crests on dorsal margin of propodus: absent (0); present (1)
38	Chelipeds with hairs on lateral surfaces of propodus near base of fingers: absent (0); present (1)
39	Chelipeds with tubercles on dorsal margin of dactylus: absent (0); present (1)
40	Pereiopods 2-5 meri with longitudinal ridge on lateral surface: absent (0); present (1)
41	Pereiopods 2-5 meri with oblique ridges on lateral surface: absent (0); present (1)

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**Table 3.** Input data matrix of 41 characters and 24 genera. The last two taxa are outgroups. Missing character states are shown by ?.

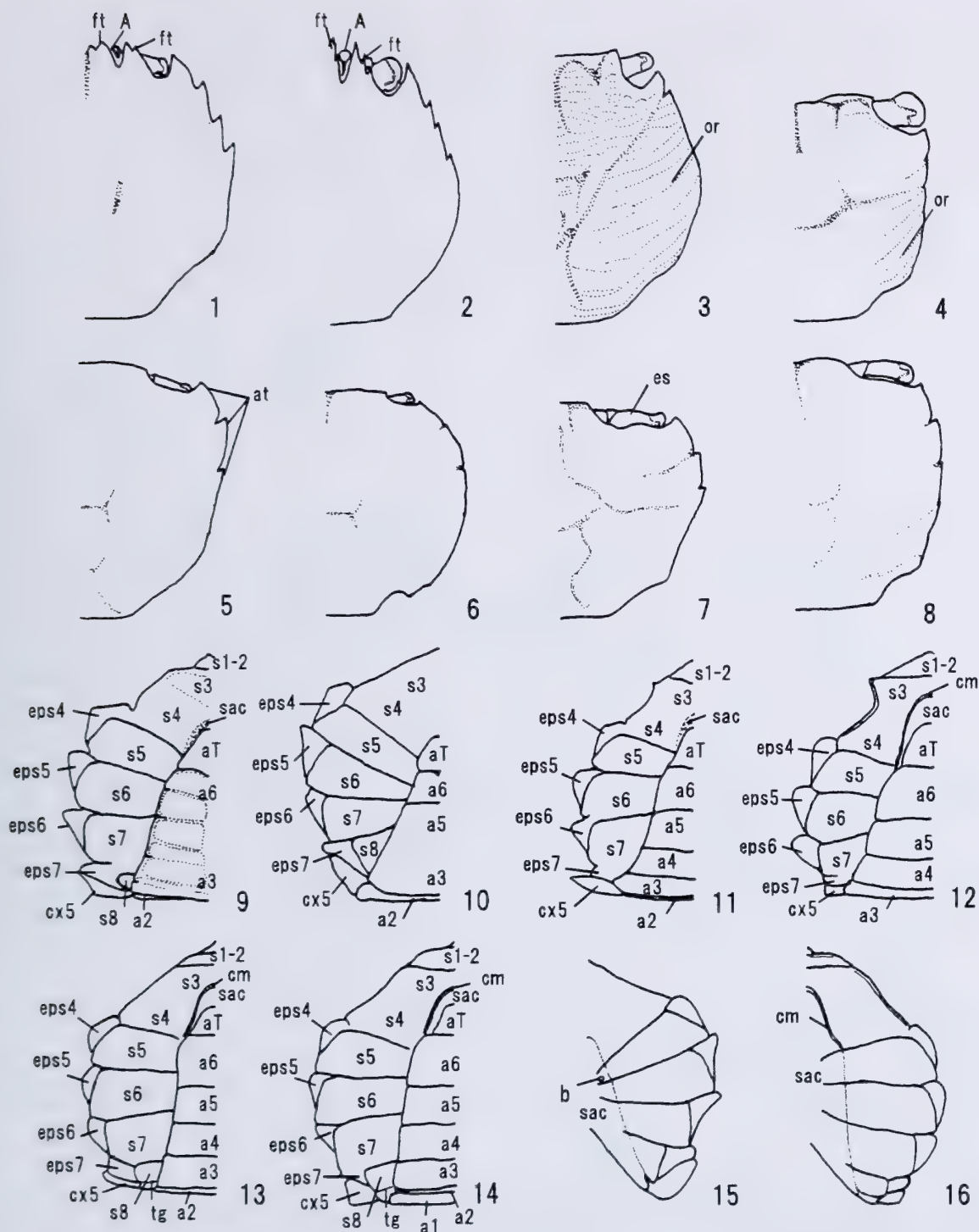
Characters	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	3	3	3	3	3	3	3	4	4											
Taxa	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1												
<i>Geograpsus</i>	0	1	1	1	0	0	1	0	0	0	0	1	1	0	1	1	0	1	1	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	1								
<i>Grapsus</i>	1	2	1	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	1	1	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	1						
<i>Metopograpsus</i>	0	1	1	1	0	0	1	1	0	0	0	0	1	0	1	1	1	0	1	0	1	1	1	0	2	1	0	0	0	0	1	1	1	0	0	0	0	1					
<i>Pachygrapsus</i>	0	1	1	1	0	0	1	1	0	0	0	0	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1				
<i>Planes</i>	2	0	1	1	0	0	1	0	0	0	0	0	1	0	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1				
<i>Chasmagnathus</i>	0	0	0	1	1	1	1	0	0	1	0	1	2	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0				
<i>Cyclograpsus</i>	0	0	0	1	0	1	1	0	0	0	0	1	2	1	1	1	1	1	1	0	1	0	1	1	1	1	2	1	0	1	1	1	1	2	2	0	0	0	0	0			
<i>Helice</i>	0	0	0	1	1	1	1	0	0	1	0	1	2	1	1	1	1	1	1	0	1	0	1	1	1	1	2	1	0	1	1	1	1	2	2	0	0	0	0	0			
<i>Metaplex</i>	0	0	0	1	1	1	1	0	0	1	0	1	2	1	1	1	1	1	1	0	1	0	1	1	1	1	2	1	0	1	1	1	1	2	2	1	0	0	0	0			
<i>Miosesarma</i>	0	0	0	1	1	1	1	0	0	1	0	1	2	?	1	1	1	?	1	0	1	?	1	1	1	?	2	1	0	1	1	1	1	2	2	1	0	?	0	0	0		
<i>Nanosesarma</i>	0	1	0	1	0	1	1	0	1	0	0	0	1	2	1	1	1	1	1	1	1	1	0	1	1	1	1	2	1	1	0	0	0	1	1	2	0	0	0	0	0		
<i>Sesarma</i>	0	1	1	1	0	1	1	0	1	0	0	0	1	2	1	1	1	1	1	1	1	1	0	1	1	1	0	2	1	1	0	0	0	1	1	2	0	1	0	1	0	1	
<i>Sesarmops</i>	1	0	0	1	0	1	1	0	1	0	0	0	0	1	2	1	1	1	1	1	1	1	0	1	1	1	1	2	1	1	0	0	0	1	1	2	0	1	0	1	0	0	
<i>Acmaeopleura</i>	0	0	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	1	0	1	1	1	2	1	0	1	1	1	1	2	2	0	0	1	0	0	0
<i>Eriocheir</i>	1	2	0	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	0	1	0	2	1	0	1	1	1	1	2	2	0	0	0	0	0	0	
<i>Gaetice</i>	0	0	0	1	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	1	0	1	1	2	1	0	1	1	1	1	2	2	0	0	0	0	0	0	
<i>Hemigrapsus</i>	0	0	0	1	1	1	1	0	0	1	0	0	1	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	2	1	0	1	1	1	1	2	2	0	0	1	0	0	0
<i>Pseudograpsus</i>	1	0	0	1	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	1	0	1	1	1	2	1	0	1	1	1	1	2	2	0	0	1	0	0	0
<i>Ptychognathus</i>	0	1	0	1	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	1	0	1	1	1	2	1	0	0	1	1	1	2	2	0	0	1	0	0	0
<i>Varuna</i>	1	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1	0	1	0	2	1	0	1	1	1	1	2	2	0	0	0	0	0	0
<i>Percnon</i>	2	2	0	0	0	0	1	0	0	0	1	2	2	0	0	1	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	1	0	1	1	2	0	0	0	0	1	0	0
<i>Plagusia</i>	2	2	0	0	0	0	1	0	0	0	1	0	2	0	0	1	0	0	0	0	1	1	0	1	1	1	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0
<i>Leptodius</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cancer</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Figures 2.12–2.16, 4.5, 4.8). Upper orbital fissures are present in both outgroup taxa (7–0), and absent in all taxa of the Grapsidae (7–1; Figures 1.1–1.8, 4.11, 4.12, 4.15). Two grapsines, *Metopograpsus* and *Pachygrapsus*, and a varunine *Acmaeopleura* possess the anterolateral margin without teeth (8–1), but all other taxa have anterolateral teeth (8–0; Figures 1.1–1.8, 4.11, 4.12, 4.15). The pterygostomian and ventrolateral surfaces in three sesarmines, *Nanosesarma*, *Sesarma*, and *Sesarmops*, are ornamented with oblique striae (9–1), while those in remaining taxa are without oblique striae (9–0). A ratio of the carapace width/length [character 1; Figure 1.1–1.8] and a maximum carapace width [character 2; Figure 1.1–1.8] are variable in examined taxa and both characters seem to be consistent at the generic level.

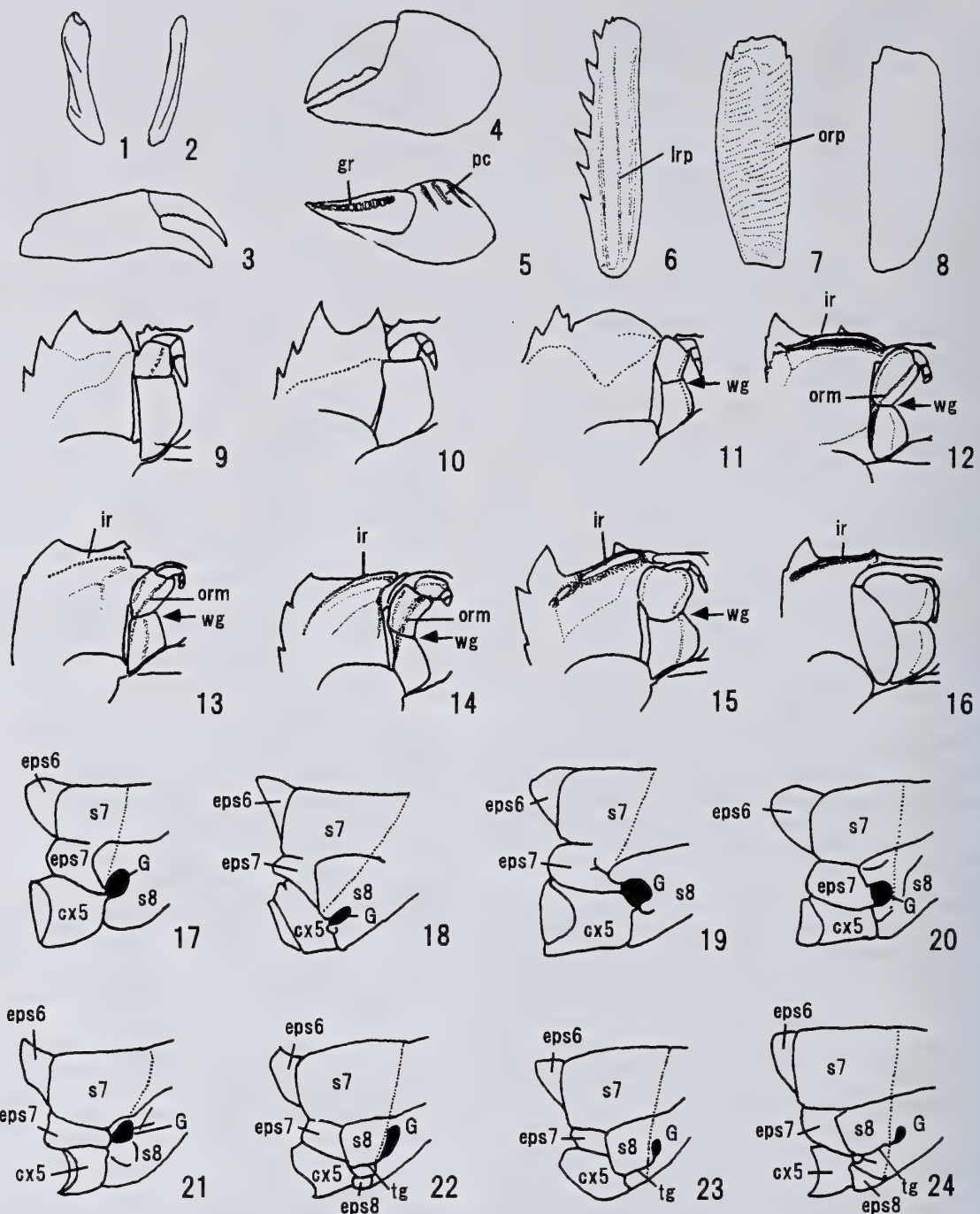
*Eye stalk and antennule.*—In examined taxa a varunine *Hemigrapsus* and three sesarmines, *Chasmagnathus*, *Metaplex* and *Miosesarma* have slender, long eye stalks (10–1; Figures 1.5, 1.7, 1.8, 4.15), but others have stout, short ones (10–0; Figure 1.1–1.4, 1.6). The antennule in all plagusiines is visible dorsally in deep clefts of the front (11–1; Figure 1.1, 1.2), and this character defines the Plagusiinae (Alcock, 1900 and subsequent workers). In all other taxa antennules are not visible dorsally (11–0; Figures 1.3–1.8, 4.11, 4.12, 4.15).

*Maxilliped 3.*—The merus is shorter than the ischium in both outgroup taxa, three grapsines, *Metopograpsus*, *Pachygrapsus* and *Planes*, a plagusiine *Plagusia*, and two varunines, *Gaetice* and *Varuna* (12–0; Figure 2.9); it is much shorter than the ischium in only plagusiine *Percnon* (12–2; Figure 2.10). In remaining taxa its length is about equal to the ischium length (12–1; Figures 2.11–2.16, 4.10). The anterolateral corner of the merus is quadrate in both outgroups (13–0), is more or less expanded and strongly convex anterolaterally in all grapsines and all varunines (13–1; Figure 2.11, 2.15, 2.16), and is not expanded but convex in all plagusiines and all sesarmines (13–2; Figures 2.9, 2.10, 2.12–2.14, 4.10). The possession of an oblique, hairy ridge on the merus and ischium is a definitive character of the Sesarminae (Alcock, 1900 and subsequent workers). In examined taxa, all extant sesarmines possess this oblique, hairy ridge (14–1; Figure 2.12–2.14), which all other taxa lack. In all grapsines, all sesarmines and a varunine *Hemigrapsus*, a wide rhomboidal gap separates maxillipeds 3 (15–1; Figure 2.11–2.15), while maxillipeds 3 are completely closed together or leave a narrow gape in all other taxa (15–0; Figures 2.9, 2.10, 2.16, 4.10). The exopods are wide in two outgroup taxa and most varunines (16–0; Figure 2.16), but narrow in most grapsines, all plagusiines and all sesarmines (16–1; Figures 2.9–2.15, 4.10). In both





**Figure 1.** Diagrammatic representation of selected extant grapsid morphological characters. 1-8. Dorsal view of carapace. 9-14. Thoracic sternum and abdomen of male. 15, 16. Thoracic sternum of male. 1, 9: *Plagusia dentipes* De Haan, 1833 (CL = 43.5 mm). 2, 10, 15: *Pernon planissimum* (Herbst, 1804) (CL = 33.8 mm). 3: *Grapsus albolineatus* Lamarck, 1818 (CL = 57.6 mm). 4: *Sesarma* (*Perisesarma*) *bidens* (De Haan, 1835) (CL = 12.5 cm). 5, 13, 16: *Hemigrapsus sanguinensis* (De Haan, 1835) (CL = 18.9 mm). 6, 13: *Cyclograpsus intermedius* Ortmann, 1894 (CL = 18.3 mm). 7: *Metaplex crenulata* (Gerstecker, 1856) (CL = 29.4 mm). 8: *Helice leachi* Hess, 1865 (CL = 14.6 mm). 12: *Sesarmops intermedium* (De Haan, 1835) (CL = 24.1 cm). **Abbreviations:** A, antennule; a1, abdominal somite 1; a2, abdominal somite 2; a3, abdominal somite 3; a4, abdominal somite 4; a5, abdominal somite 5; a6, abdominal somite 6; aT, telson; at, anterolateral tooth; b, button; cm, cristiform margin of anterior sterno-abdominal cavity; cx5, coxa of pereopod 5; eps4, episternite 4; eps5, episternite 5; eps6, episternite 6; eps7, episternite 7; es, eye stalk; ft, frontal tooth; or, oblique ridge; s1-2, thoracic sternites 1-2; s3, thoracic sternite 3; s4, thoracic sternite 4; s5, thoracic sternite 5; s6, thoracic sternite 6; s7, thoracic sternite 7; s8, thoracic sternite 8; sac, sterno-abdominal cavity; tg, transverse groove on sternite 8.



**Figure 2.** Diagrammatic representation of selected extant grapsid morphological characters. 1, 2. Gonopod 1. 3-5. Cheliped. 6-8. Merus of pereopod 4. 9-16. Ventral view of carapace and maxilliped 3. 17-24. Thoracic sternites 7 and 8. 1, 11, 19: *Grapsus tenuicrustatus* (Herbst, 1783) (CL = 36.1 mm). 2, 13, 23: *Cyclograpsus intermedius* Ortmann, 1894 (CL = 18.3 mm). 4, 5: *Sesarma* (*Parasesarma*) *pictum* (De Haan, 1835) (CL = 17.4 mm). 6, 9, 17: *Plagusia dentipes* De Haan, 1833 (CL = 43.5 mm). 7: *Grapsus albolineatus* Lamarck, 1818 (CL = 57.6 mm). 8: *Helice leachi* Hess, 1865 (CL = 14.6 mm). 10, 18: *Percnon planissimum* (Herbst, 1804) (CL = 33.8 mm). 12, 20: *Sesarmops intermedium* (De Haan, 1835) (CL = 24.1 mm). 14, 24: *Metaplex crenulata* (Gerstecker, 1856) (CL = 29.4 mm). 15, 22: *Hemigrapsus sanguinensis* (De Haan, 1835) (CL = 18.9 mm). 16: *Ptychognathus* sp. aff. *P. ishii* Sakai, 1939 (CL = 8.3 mm). 21: *Chasmagnathus convexus* De Haan, 1833 (CL = 40.1 mm). **Abbreviations:** cx5, coxa of pereopod 5; eps6, episternite 6; eps7, episternite 7; eps8, episternite 8; G, gonopore; gr, tubercles on dorsal margin of dactylus; ir, infraorbital ridge; lrp, longitudinal ridge on lateral surface of pereopod 4; orm, oblique, hairy ridge on merus and ischium of maxilliped 3; orp, oblique ridge on lateral surface of pereopod 4; pc, pectinated crests on dorsal margin of propodus; s7, thoracic sternite 7; s8, thoracic sternite 8; tg, transverse groove on sternite 8; wg, wide rhomboidal gap between maxillipeds 3.



outgroup taxa and all plagusiines the palp articulates at an anteromesial angle of the merus (17-0; Figure 2.9, 2.10); however, in all other taxa it articulates at an anterior margin (17-1; Figures 2.11-2.16, 4.10). The dactyli are long in both outgroup taxa, all plagusiines, all grapsines and all varunines (18-0; ; Figure 2.9-2.11, 2.15, 2.16), but is reduced and short in all extant sesarmines (18-1; Figure 2.12-2.14).

**Abdomen.**—In all grapsines, all sesarmines and all varunines, the male abdomen consists of seven unfused abdominal somites (19-1; Figures 1.11-1.14, 4.9, 4.14), while the outgroup taxa and all plagusiines possess fused somites (19-0; Figure 1.9, 1.10). The outgroup taxa, most varunines and four sesarmines, *Cyclograpsus*, *Helice*, *Metaplex* and *Miosesarma*, have a narrow male abdomen (20-0; Figures 1.13, 1.14, 4.3, 4.9, 4.14), while the male abdomen is wide and fills the entire space between pereopods 5 in all grapsines, all plagusiines, two varunines, *Varuna* and *Eriocheir*, and three sesarmines, *Nanosesarma*, *Sesarma* and *Sesarmops* (20-1; Figure 1.9-1.12).

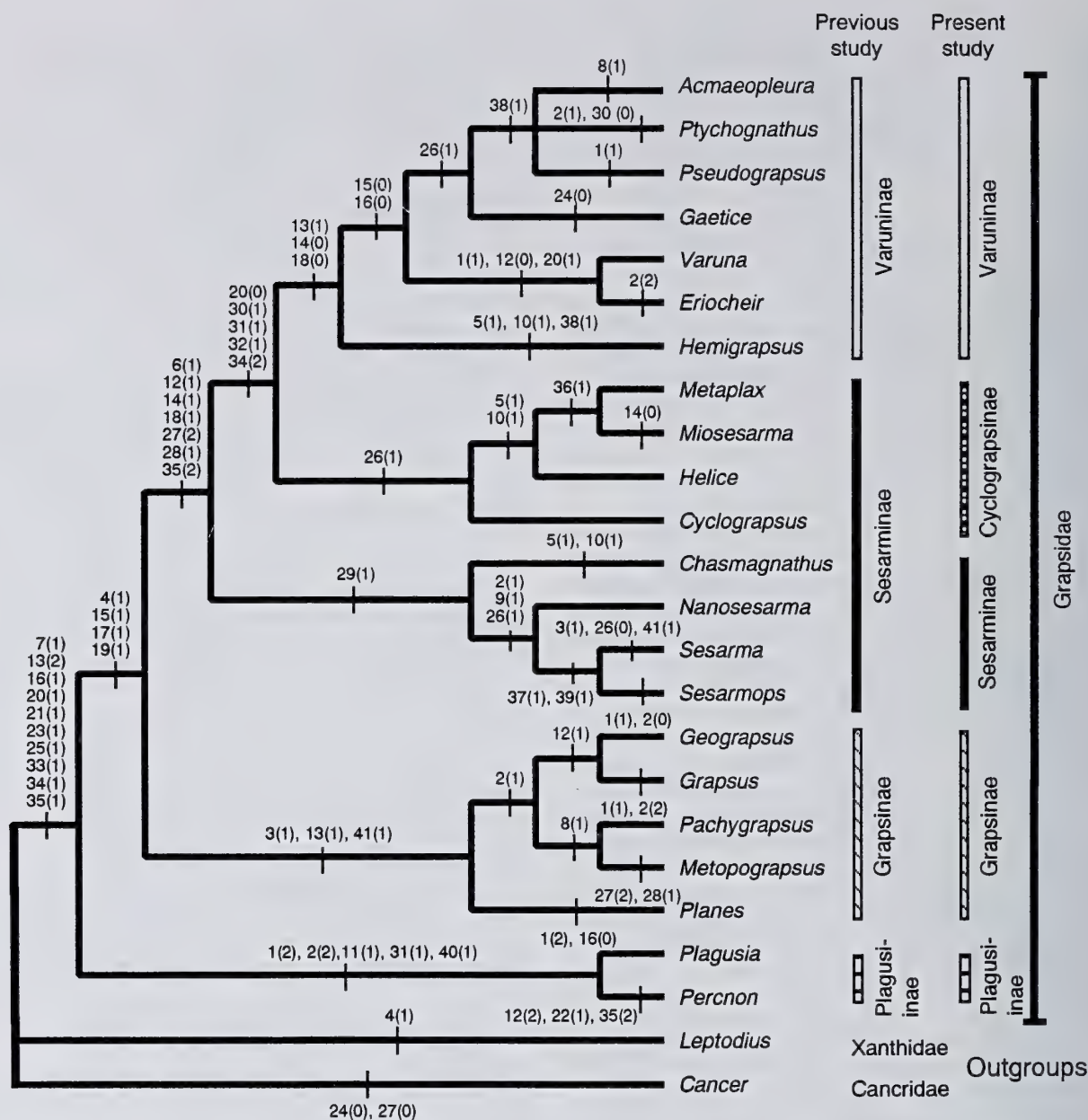
**Thoracic sternum.**—All grapsids possess a wide thoracic sternum (21-1; Figures 1.9-1.14, 4.2, 4.3, 4.6, 4.7, 4.9, 4.10, 4.13, 4.14, 4.16), but the two outgroup taxa have a narrow sternum (21-0). In the outgroup taxa and most extant grapsids, thoracic sternites 1-2 are distinct (22-0; Figure 1.9, 1.11-1.14), while in only plagusiine *Percnon* they are reduced and indistinct (22-1; Figure 1.10). In both outgroup taxa, a suture between sternites 2 and 3 is distinct and well defined as a deep groove (23-0); however, the suture in all grapsids is indistinct and poorly defined (23-1; Figures 1.9-1.14, 4.13, 4.14). A median groove on sternite 3 is present in one outgroup taxon, *Cancer*, and a varunine *Gaetice* (24-0), but it is absent in all other examined taxa (24-1; Figures 1.9-1.14, 4.6, 4.13). A median groove on sternite 4 is present in both outgroup taxa (25-0), but is absent in all grapsid taxa (25-1; Figures 1.9-1.14, 4.6). Guinot and Bouchard (1998) described the button on the male thoracic sternum within the Brachyura and indicated that in their examined material plagusiines and grapsines possessed the button on the sternum (Figure 1.15), but that the button was either present or absent within the Varuninae and Sesarminae (Figures 1.16, 4.6). In our examined material the button [character 26] is present in both outgroup taxa, all grapsines and all plagusiines, and present or absent in sesarmines and varunines. The outgroup taxon, *Cancer*, possesses a shallow sterno-abdominal cavity (27-0), while all other examined taxa have a deep sterno-abdominal cavity (Figures 1.9-1.16, 4.6). The anterior end of the sterno-abdominal cavity reaches the anterior sternite 4 in one outgroup, *Leptodius*, most grapsines and all plagusiines (27-1; Figure 1.9-1.11, 1.15), and reaches sternite 3 in all sesarmines, all varunines and a grapsine *Metopograpsus* (27-2; Figures 1.12-1.14, 1.16, 4.6, 4.13, 4.14). Guinot and Bouchard (1998) mentioned that in the Thoracotremata a deep sterno-abdominal cavity was often anteriorly delimited by a cristiform margin. In our examined material, the cristiform margin is well defined in all sesarmines, all varunines and a grapsine *Metopograpsus* (28-1; Figures 1.12-1.14, 1.16, 4.6, 4.13), but absent in both outgroup taxa, all plagusiines and most grapsines (28-0; Figure 1.9-1.11,

1.15). *Nanosesarma*, *Sesarma* and *Sesarmops*, members of the Sesarminae, possess deeply concave lateral margins of sternites 3-4 (29-1; Figure 1.12). In both outgroup taxa and the sesarmine genera, *Chasmagnathus*, *Nanosesarma*, *Sesarma* and *Sesarmops*, the male abdomen covers entirely the sternite 8 (31-0, 32-0; Figure 1.9-1.12). The sternite 8 is not covered entirely by the abdomen and is visible in ventral and posterior view in all varunines and four sesarmines, *Cyclograpsus*, *Helice*, *Metaplex* and *Miosesarma* (31-1, 32-1; Figures 1.13, 1.14, 4.14), but in both plagusiine taxa the male abdomen fills the entire space between pereopods 5 (31-0; Figure 1.9, 1.10) and is visible in ventral view (32-1; Figure 1.9, 1.10).

In members of the section Heterotremata Guinot, 1977, male gonopores are located on coxae and/or the thoracic sternite 8, and the gonopores in all representatives within the Thoracotremata Guinot, 1977 are on sternite 8 (Guinot, 1977; Guinot and Richer de Forges, 1997). If male gonopores are situated on the inner part of sternite 8, the sternite is traversed by a groove which arises from the coxa and joins the gonopore or is interrupted (Figure 2.22-2.24) (Guinot, 1979; Tavares, 1992; Jamieson, Guinot and Richer de Forges, 1996). Both outgroups, all grapsines, all plagusiines, and the sesarmine genera, *Chasmagnathus*, *Nanosesarma*, *Sesarma* and *Sesarmops*, lack a transverse groove on the sternite 8 (30-0; Figure 2.17-2.20); however, most varunines and four sesarmines, *Cyclograpsus*, *Helice*, *Metaplex* and *Miosesarma*, have a groove on sternite 8 (30-1; Figures 2.22-2.24, 4.13, 4.14). In all grapsids of the Thoracotremata male gonopores are opened on thoracic sternite 8 (34-1; Figures 2.17-2.24, 4.13, 4.14), but in both outgroup taxa belonging to the Heterotremata they are located on the coxae (34-0). When male gonopores are situated on sternite 8, they are opened on lateral parts of sternite 8 in all plagusiines, all grapsines and the sesarmines, *Chasmagnathus*, *Nanosesarma*, *Sesarma* and *Sesarmops* (34-1; Figure 2.17-2.21). The male gonopores are located on the inner part of sternite 8 (34-2; Figures 2.22-2.24, 4-13, 4.14) in all varunines and the sesarmines, *Cyclograpsus*, *Helice*, *Metaplex* and *Miosesarma*.

**Gonopod.**—Only one character is found to be informative. Male gonopods 1 are sinuous (35-0) in both outgroup taxa, twisted (35-1; Figure 2.1) in a plagusiine *Plagusia* and all grapsines, and linear (35-2; Figures 2.2, 4.7, 4.13, 4.14, 4.16) in a plagusiine *Percnon*, all sesarmines and all varunines.

**Pereopods.**—Two sesarmine genera, *Metaplex* and *Miosesarma*, possess a slender, elongate palm of the male chelipeds (36-1; Figures 2.3, 4.4), while all other taxa possess a short, massive palm (36-0; Figure 2.4). In examined material two sesarmines, *Sesarma* and *Sesarmops*, have chelipeds with pectinated crests on the dorsal margin of the propodus (37-1; Figure 2.5) and with tubercles on the dorsal margin of the dactylus (39-1; Figure 2.5). Four varunines, *Acmaeopleura*, *Hemigrapsus*, *Pseudograpsus* and *Ptychognathus*, bear hairs on the lateral surface of the propodus of the cheliped near the base of fingers (38-1), which all other extant taxa lack. Longitudinal ridges on the lateral surface of meri of pereopods 2-5 are present in the Plagusiinae (40-1; Figure 2.6), but absent in all other taxa (40-0; Figures



**Figure 3.** Single parsimonious tree of 22 genera within the Grapsidae. Length = 85, Consistency index = 0.565, Retention index = 0.807, Rescaled consistency index = 0.456. Character changes are indicated.

2.8, 4.15). All taxa within the Grapsinae and a sesarine *Sesarma* possess oblique ridges on the lateral surface of meri of pereopods 2–5 (41–1; Figure 2.7), which all other taxa lack.

### Results

The present analysis yielded a single parsimonious tree, 85 steps long with a consistency index (CI) of 0.565, a retention index (RI) of 0.807 and a rescaled consistency index (RC) of 0.456 (Figure 3). The monophyly of the Grapsidae is well supported by ten characters, five of which are unique

and unreversed: the upper orbital margin without distinct notches (7–1), a wide thoracic sternum (21–1), the absence of a suture between thoracic sternites 3 and 4 (23–1), the absence of a median groove on the thoracic sternite 4 (25–1), and male gonopores opened on thoracic sternites 8 (33–1). Our analysis suggests that within the Grapsidae the Plagusiinae is the most basal clade, followed by the Grapsinae, Sesarinae and the most derived Varuninae. The Plagusiinae is united by five characters, three of which are unique: antennules which are visible dorsally (11–1), sternite 8 which is visible ventrally (31–1), and the posses-



sion of longitudinal ridges on meri of pereopods 2–5 (40–1).

The Grapsinae+Sesarminae+Varuninae clade is unambiguously united by four synapomorphies, three of which are never reversed: the absence of frontal teeth (4–1), the palp of the maxilliped 3 which articulates at an anterior margin of the merus (17–1), and the male abdomen with seven free somites (19–1). Three synapomorphies, the carapace with oblique ridges dorsally (3–1), an expanded anterolateral corner of the merus of the maxilliped 3 (13–1), and the presence of meri of pereopods with oblique ridges on the lateral surface (41–1), well support the monophyly of the Grapsinae. The analysis shows the sister-group relationship of the Grapsinae and Sesarminae+Varuninae clades. The Sesarminae+Varuninae clade is unambiguously united by seven characters of which four are never reversed: the possession of the infraorbital ridge (6–1), an anterior margin of the sterno-abdominal cavity reaching the thoracic sternite 3 (27–2), the presence of the cristiform margin of an anterior sterno-abdominal cavity (28–1), and linear gonopods 1 (35–2).

Our analysis suggests that the Sesarminae as customarily defined is a polyphyletic group. The monophyly of the *Chasmagnathus*+*Nanosesarma*+*Sesarma*+*Sesarmops* clade is united by only one character, deeply concave lateral margins of thoracic somites 3 and 4 (29–1), and is derived as the sister to the Varuninae+four remaining sesarmines (*Cyclograpsus*, *Metaplex*, *Helice*, *Miosesarma*) clade. The Varuninae and *Metaplex*+*Miosesarma*+*Helice*+*Cyclograpsus* clades are unambiguously united by four unique synapomorphies: the presence of a transverse groove on the thoracic sternite 8 (30–1), the thoracic sternite 8 which is visible in ventral and posterior view (31–1, 32–1), and male gonopores located on the inner part of the thoracic sternite 8 (34–2). The Varuninae clade is the sister to the *Metaplex*+*Miosesarma*+*Helice*+*Cyclograpsus* clade and is united by three characters, an expanded anterolateral corner of the merus of maxilliped 3 (13–1), the absence of oblique, hairy ridges on the merus and ischium of maxilliped 3 (14–0) and a long dactylus of maxilliped 3 (18–0).

## Discussion

The family Grapsidae is presently divided into four subfamilies, Grapsinae, Plagusiinae, Sesarminae and Varuninae, based on the adult morphology (i.e., Alcock, 1900, Rathbun, 1918, Sakai, 1976, Guinot, 1979, Manning and Holthuis, 1981). However, the subfamilial arrangement of some genera within the Grapsidae has been questioned by recent contributions based on larval morphology (Pereyra Lago, 1993, Schubart and Cuesta, 1998 and many more) and molecular data using the 16S rRNA (Schubart *et al.*, 2000). Guinot and Bouchard (1998) mentioned that both Sesarminae and Varuninae were artificial groups. Rice (1980) noted that the Grapsinae seemed to have the most advanced zoeae within the Grapsidae and thought that the four subfamilies within the Grapsidae evolved independently from a more primitive stock of which there is no larval evidence. Schubart, Neigel and Felder (2000) and Schubart *et al.* (2000) provided molecular phylogenies of the Grapsidae. Although Schubart *et al.* (2000) treated four subfamilies within the Grapsidae as families, we place four

subfamilies within the Grapsidae according to previous studies of Alcock (1900), Sakai (1976), Manning and Holthuis (1981) and others.

The adult morphology-based phylogeny presented herein and the molecular phylogeny of Schubart *et al.* (2000) each of which supports monophyly of the Grapsidae, are each largely supported, but they differ somewhat in topology. Ten characters, five of which are unique and unreversed, well support the monophyly of the family Grapsidae in this study. Schubart, Neigel and Felder (2000) showed the paraphyly of the family based on molecular data using 16S rRNA but the subsequent study of Schubart *et al.* (2000) suggested the monophyly of the family; we concur that the Grapsidae is monophyletic.

Our morphology-based phylogenetic analysis suggests the Plagusiinae is the earliest derived crown-group subfamily, followed by the Grapsinae. These results support the molecular phylogeny of the family by Schubart *et al.* (2000). The Plagusiinae and Grapsinae are monophyletic by our analysis. The monophyly of the Grapsinae is well supported by molecular data (Schubart *et al.*, 2000) and larval morphology (Rice, 1980, Cuesta and Schubart, 1999). Schubart *et al.* (2000) showed that the Plagusiinae was polyphyletic and that only *Percnon* was the most basal clade. However, the larval morphology of *Percnon* is most similar to that of *Plagusia* within the Grapsidae (Rice, 1980) which supports our tree in which *Percnon* and *Plagusia* occur together on one clade.

The subfamily Sesarminae is polyphyletic. The *Metaplex*+*Miosesarma*+*Helice*+*Cyclograpsus* clade is readily distinguished from the *Chasmagnathus*+*Nanosesarma*+*Sesarma*+*Sesarmops* clade by having four unique synapomorphies and the former is derived as the sister to the Varuninae clade. One unique synapomorphy supports the monophyly of the latter sesarmine clade. The Sesarminae was previously discriminated from the other three subfamilies by the possession of an oblique, hairy ridge on the merus and ischium of the maxilliped 3 (Alcock, 1900 and subsequent workers). In our analysis the presence of this ridge [character 14] is not a unique character and the character state in the Varuninae clade is the absence of the ridge, a reversal of the state identified as a synapomorphy of the Sesarminae+Varuninae clade. Guinot (1979) indicated that male gonopores of *Cyclograpsus*, *Helice* and *Metaplex* together with those of varunine genera were located on the inner part of thoracic sternite 8. Examination of American sesarmine genera based on molecular data (Schubart *et al.*, 2000) suggested that *Chasmagnathus* and *Cyclograpsus* should be classified within the Varuninae and that the remaining Sesarminae group was monophyletic. Pereyra Lago (1993) and Schubart and Cuesta (1998) also showed that larval characters of three genera, *Chasmagnathus*, *Cyclograpsus* and *Helice*, were similar to those of members within the Varuninae rather than *Sesarma* sensu lato. However, our adult-morphology based analysis indicates that *Chasmagnathus* remains within the "Sesarminae" clade and that *Cyclograpsus* and *Helice* belong to another clade which is derived as the sister to the Varuninae clade and are more derived than the "Sesarminae" clade.

The present analysis separates the *Metaplex*+*Miose-*



*sarma*+*Helice*+*Cyclograpsus* clade from the "Sesarminae" clade and strongly suggests that genera placed within the clade should be classified in another subfamily. H. Milne Edwards (1853) erected a new tribe Cyclograpscaea within his subfamily Grapsinae (= Grapsidae see Alcock, 1900). Six genera, *Pseudograpsus*, *Heterograpsus* Lucas, 1849 (= *Brachynotus* de Haan, 1833), *Cyclograpsus*, *Paragrapsus* H. Milne Edwards, 1853, *Pralynotus* de Haan, 1835 (= *Gaetice*), and *Chasmagnathus* were originally included in the Cyclograpscaea. Subsequently, Alcock (1900) redefined four subfamilies within the Grapsidae, and synonymized the Cyclograpscaea with the Sesarminae and Varuninae. He moved *Pseudograpsus*, *Brachynotus* and *Gaetice* to the Varuninae and *Cyclograpsus* and *Chasmagnathus* to the Sesarminae. Tesch (1918) referred *Paragrapsus* to the Sesarminae. In our phylogenetic analysis, *Pseudograpsus* and *Gaetice* are classified within the Varuninae, and *Chasmagnathus* is placed within the Sesarminae. Two genera, *Brachynotus* and *Paragrapsus*, were not examined in our analysis. We treat the tribe Cyclograpscaea which contains a remaining genus *Cyclograpsus* as a subfamily Cyclograpsinae H. Milne Edwards, 1853 *nomen. transl. herein* (type genus: *Cyclograpsus* by present designation). Three additional genera, *Helice*, *Miosesarma* and *Metaplex* are included in the Cyclograpsinae based on the present analysis. The Cyclograpsinae is distinguished from the Sesarminae in that male gonopores are located on the inner part of thoracic sternite 8, sternite 8 is visible in ventral and posterior view, and bears a distinct transverse groove that extends from the articulation of the coxa-sternal junction to the gonopore. The present subfamily differs from the Varuninae derived as its sister group by the presence of an oblique, hairy ridge on the merus and ischium and a short, reduced dactylus of maxilliped 3, and the absence of an anterolateral expansion of the merus of maxilliped 3. *Paragrapsus* and *Heterograpsus* Campbell and Griffin, 1966 have an oblique, hairy ridge on the merus and ischium of maxilliped 3, male gonopores located on the inner part of the thoracic sternite 8, and a transverse groove on sternite 8; therefore, it is suggested that both genera should be referred to the Cyclograpsinae.

Within examined material the Varuninae is at least monophyletic. However, Schubart *et al.* (2000) showed using molecular data that the subfamily was polyphyletic, *Euchirograpsus* H. Milne Edwards, 1853, a non North-western Pacific genus, was the sister taxon of *Plagusia*, and *Platychirograpsus* de Man, 1896 and *Glyptograpsus* Smith, 1870, which both are American endemic genera, were derived as the sister to the Sesarminae. The reexamination of the systematic position of these three genera is beyond the scope of our study, whilst examination of the detail adult morphology would be necessary to confirm the reassignment of these genera.

The location of gonopores on thoracic sternite 8 [character 34] and the possession of the infraorbital ridge [character 6] are supported as useful phylogenetic characters. The gonopores are located on the lateral margin of sternite 8 in the Plagusiinae, Grapsinae and Sesarminae, and on the inner part of sternite 8 in the Cyclograpsinae and Varuninae.

The Plagusiinae and Grapsinae lack the infraorbital ridge, while the Sesarminae, Cyclograpsinae and Varuninae possess the infraorbital ridge.

The following diagnosis is given for five subfamilies based on our phylogenetic analysis:

*Subfamily Plagusiinae* Dana, 1851.—Front with teeth. Antennule visible dorsally. Infraorbital ridge absent. Maxillipeds 3 without wide rhomboidal gap and oblique, hairy ridge on merus and ischium; anterolateral corner not expanded, convex; palp articulating at anteromesial corner of merus; exopod narrow. Male abdomen wide, filling entire space between pereopods 5. Anterior margin of sterno-abdominal cavity reaching thoracic sternite 4. Sternal button present in male. Male gonopore located on lateral margin of thoracic sternite 8. Meri of pereopods usually bearing longitudinal ridges laterally and spines dorsally (modified from Rathbun, 1918).

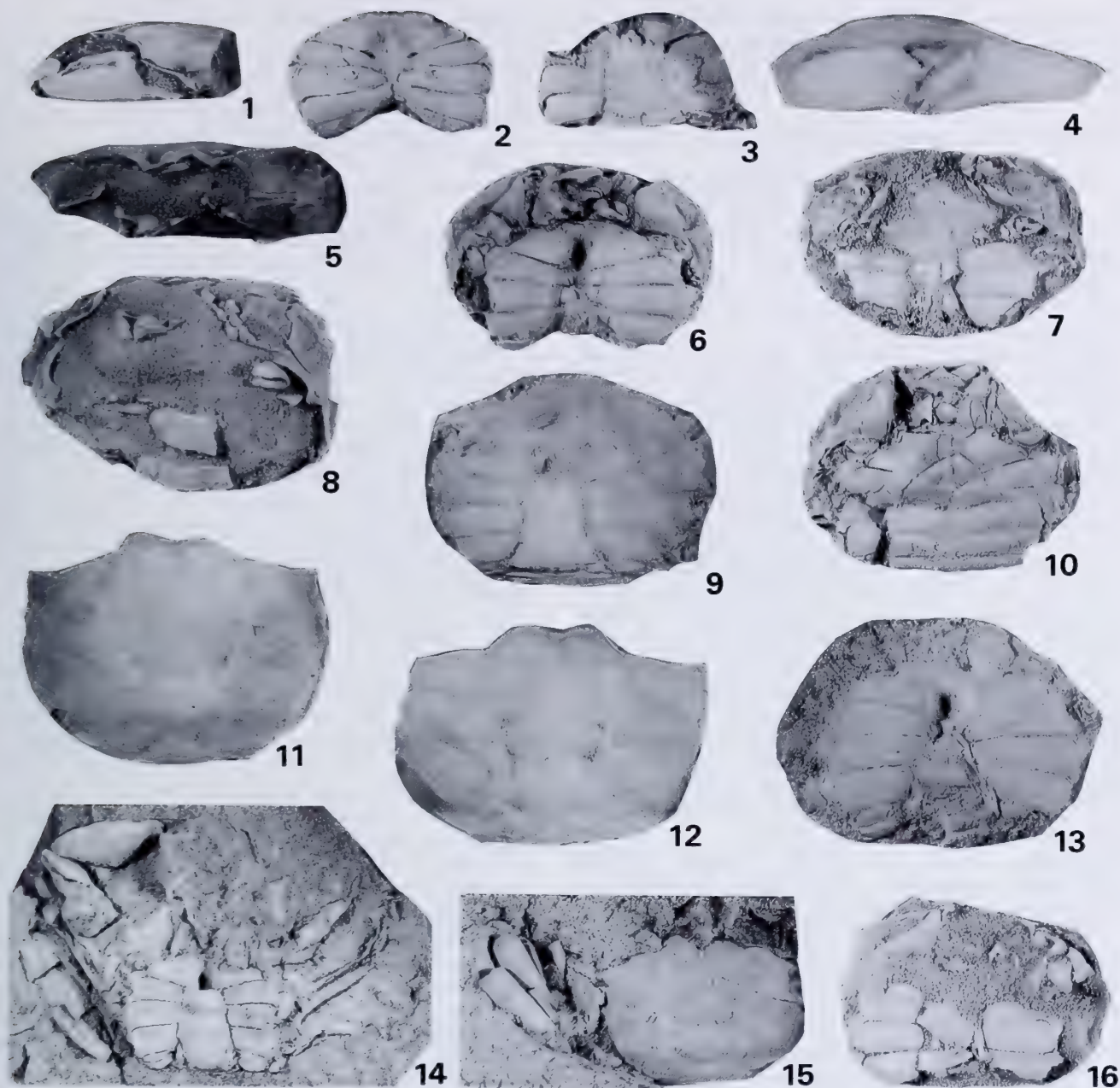
*Subfamily Grapsinae* MacLeay, 1838.—Front usually strongly deflexed. Carapace usually with oblique ridges dorsally. Infraorbital ridge absent. Maxillipeds 3 usually separated by wide rhomboidal gap, without oblique, hairy ridge on merus and ischium; anterolateral corner of merus usually expanded; palp articulating at anterior margin of merus; exopod narrow. Male abdomen wide, filling entire space between pereopods 5. Anterior margin of sterno-abdominal cavity usually reaching thoracic sternite 4. Sternal button present in male. Male gonopore located on lateral margin of thoracic sternite 8 (modified from Rathbun, 1918).

*Subfamily Sesarminae* Dana, 1851.—Front strongly deflexed. Infraorbital ridge present. Maxillipeds 3 separated by wide rhomboidal gap, and with oblique, hairy ridge on merus and ischium; anterolateral corner of merus not expanded, convex; palp articulating at anterior margin of merus; exopod narrow. Male abdomen wide, filling entire space between pereopods 5. Anterior margin of sterno-abdominal cavity reaching thoracic sternite 3. Sternal button present or absent in male. Male gonopore located on lateral margin of thoracic sternite 8 (modified from Rathbun, 1918).

*Subfamily Varuninae* H. Milne Edwards, 1853.—Front moderately or little deflexed. Infraorbital ridge present. Maxillipeds 3 moderately or slightly gaping, without oblique, hairy ridge on merus and ischium; anterolateral corner of merus expanded; palp articulating at anterior margin of merus; exopod usually wide. Male abdomen rarely filling entire space between pereopods 5. Anterior margin of sterno-abdominal cavity reaching thoracic sternite 3. Transverse groove usually present on sternite 8. Sternal button usually present in male. Male gonopore located on inner part of thoracic sternite 8 (modified from Rathbun, 1918).

*Subfamily Cyclograpsinae* H. Milne Edwards, 1853 [nom. transl. of Tribe Cyclograpscaea].—Front strongly deflexed. Infraorbital ridge present. Maxillipeds 3 separated by wide rhomboidal gap, with oblique, hairy ridge on merus and ischium; anterolateral corner of merus not expanded, convex; palp articulating at anterior margin of merus; exopod narrow. Male abdomen not filling entire space between pereopods 5. Anterior margin of sterno-abdominal cavity





**Figure 4.** 1-13, 15, 16. *Miosesarma japonicum* Karasawa, 1989. 1: MFM83343, middle Miocene Masuda Group, frontal view of carapace and lateral view of cheliped, female,  $\times 2.5$ . 2: MFM39154, middle Miocene Bihoku Group, ventral view of thoracic sternum, female,  $\times 2.5$ . 3: MFM39155, middle Miocene Bihoku Group, ventral view of thoracic sternum and abdomen, male,  $\times 2.5$ . 4: MFM9146, lower Miocene Mizunami Group, lateral view of chelipeds, male,  $\times 1.5$ . 5: MFM83344, middle Miocene Masuda Group, frontal view of carapace, male,  $\times 2.5$ . 6: MFM39156, middle Miocene Bihoku Group, ventral view of carapace, thoracic sternum and maxillipeds 3, male,  $\times 2.5$ . 7: MFM83345, middle Miocene Masuda Group, ventral view of carapace, thoracic sternum and gonopods 1, male,  $\times 2.5$ . 8: MFM83344, middle Miocene Masuda Group, ventral view of carapace and abdomen, male,  $\times 2.5$ . 9: MFM9017 (paratype), lower Miocene Mizunami Group, ventral view of thoracic sternum and abdomen, male,  $\times 2.5$ . 10: MFM39157, middle Miocene Bihoku Group, ventral view of carapace, thoracic sternum, abdomen and maxillipeds 3, female,  $\times 2.5$ . 11: MFM9016 (paratype), lower Miocene Mizunami Group, dorsal view of carapace, male,  $\times 2.5$ . 12: MFM9015 (holotype), lower Miocene Mizunami Group, dorsal view of carapace, male,  $\times 2.5$ . 13: MFM9147, lower Miocene Mizunami Group, ventral view of thoracic sternum, abdomen and gonopods 1, male,  $\times 2.5$ . 15: MFM39158, middle Miocene Bihoku Group, dorsal view of carapace and eye stalk, and lateral view of pereopods, male,  $\times 2.5$ . 16: MFM83346, middle Miocene Masuda Group, ventral view of carapace, thoracic sternum, abdomen and gonopods 1, male,  $\times 2.5$ . 14. *Miosesarma naguraense* Kato, 1996, MFM83347, middle Miocene Nagura Formation, ventral view of thoracic sternum, abdomen and gonopods 1, male,  $\times 1.5$ .



reaching thoracic sternite 3. Transverse groove present on sternite 8. Sternal button usually absent in male. Male gonopore located on inner part of thoracic sternite 8 (redefined here).

### Redefinition of the genus *Miosesarma* Karasawa, 1989

Subfamily Cyclograpsinae H. Milne Edwards, 1853

Genus *Miosesarma* Karasawa, 1989

*Type species.*—*Miosesarma japonica* Karasawa, 1989 by monotypy.

*Species included.*—*Miosesarma japonicum* Karasawa, 1989 (Figure 4.1–4.13, 4.15, 4.16) and *Miosesarma naguraense* Kato, 1996 (Figure 4.14).

*Revised diagnosis.*—Carapace rectangular in outline, length about 3/4 width, widest at midlength. Front deflexed, about 1/4 carapace width. Frontal margin bilobed. Upper orbital margin sinuous, occupying about 3/4 carapace width. Anterolateral margins nearly straight, almost parallel, with 4 forwardly directed teeth. Posterolateral margin sinuous. Dorsal surface smooth, moderately vaulted transversely and weakly vaulted longitudinally. Regions well defined; epibranchial lobe more inflated; mesobranchial lobe with ridge extending from 4th anterolateral tooth; metabranchial lobe with weak ridge parallel to posterolateral margin. Infraorbital ridge present with prominence laterally. Thoracic sternum wide; sterno-abdominal cavity of male deep, reaching sternite 3; sternite 8 of male with transverse groove. Male abdomen narrow, not filling entire space between pereopods 5. Merus of maxilliped 3 subequal to ischium with convex anterolateral margin; exopod narrow. Male gonopod linear; gonopore opened on inner part of thoracic sternite 8. Chelipeds dissimilar in both sexes; female chelae much smaller than male; propodus slender, elongate. Pereopods flattened.

*Remarks.*—Karasawa (1989) originally placed *Miosesarma* in the subfamily Sesarminae. Examination of new specimens shows that the genus is referred to the subfamily Cyclograpsinae because the infraorbital ridge is present, the gonopore is located on the inner part of the thoracic sternite 8, a narrow male abdomen does not fill all of the space between pereopods 5, and the merus of maxilliped 3 has a convex anterolateral margin. Karasawa (1989) showed that the genus had close affinities with Recent cyclograpsines, *Helice* and *Metaplex*. Our phylogenetic analysis also suggests that *Miosesarma* and *Metaplex* are sister taxa nested as the most derived clade, followed by *Helice* and the most basal *Cyclograpsus* within the Cyclograpsinae.

Most extant members of the Grapsidae live in intertidal waters and adapt to freshwater or terrestrial habitats (Guinot and Bouchard, 1998); however, *Planes* is known from pelagic waters (Manning and Holthuis, 1981) and *Euchirograpsus* from depths between 10 and 359 m (Manning and Holthuis, 1981). *Miosesarma* appears to have inhabited sublittoral and upper bathyal waters based on associated decapods and molluscs (Karasawa, 1993; Kato, 1996).

*Distribution.*—Early-early Middle Miocene of Honshu, Japan; Ayugawa Group (Karasawa, 1997), Bihoku Group

(Karasawa, 1993), Hokutan Group (Karasawa, 1997), Katsuta Group (Karasawa, 1993), Masuda Group (Karasawa, 1993), Mizunami Group (Karasawa, 1989), Chichibumachi Group (Kato, 1996), Nenokami Sandstone Member (Kato, 1996), Numanouchi Formation (Kato in prep.), Yatsuo Group (Karasawa, 1993).

### A review of fossil records of the family Grapsidae

Previously known fossil records within the family Grapsidae have included 34 species and 21 genera. Fossil records of the Grapsinae comprise three genera: *Metopograpsus* from the lower Miocene of Hungary (Müller, 1998); *Pachygrapsus* from the middle Miocene of Hungary and Poland (Müller, 1974, 1996) and from the Pleistocene of Jamaica (Morris, 1993); and *Planes* from the lower Miocene of the Caucasus (Smirnov, 1929; Glaessner, 1969).

The genus *Sesarma* (s.l.) of the Sesarminae is represented by three fossil species, *Sesarma paraensis* Beurlen, 1958, from the upper Oligocene-lower Miocene of Brazil, *Sesarma smithi* H. Milne Edwards, 1853, from the Pleistocene of Australia (Etheridge and McCulloch, 1916) and *Sesarma* sp. from the middle Miocene of Japan (Karasawa, 1993). According to Serène and Soh's 1970 reclassification of the genus *Sesarma* (s.l.), *S. smithi* now belongs to *Neosarmatium* Serène and Soh, 1970.

Varunine genera known as fossils are *Brachynotus* from the middle Miocene of Hungary (Müller, 1974), *Eriocheir* from the Pliocene of Japan (Karasawa and Narita, 2000), *Hemigrapsus* from the Pleistocene of U.S.A. (Rathbun, 1926), *Miograpsus* Fleming, 1981 from the upper Miocene of New Zealand, *Varuna* from the middle Eocene of Jamaica (Withers, 1924), and *Utica* White, 1847 from the Pleistocene of Australia (Wintle, 1886). Among these genera *Miograpsus* is the only known extinct genus.

Glaessner (1969) showed that *Telphusograpsus* Lörentz, 1902, from the Eocene of Rumania, was referable to *Varuna*; however, *Telphusograpsus* is an independent genus by virtue of having an inflated carapace with two upper orbital fissures and with a distinct inner orbital angle, and lacking a posterolateral facet on the branchial region. Members of the Grapsidae lack a distinct inner orbital angle and upper orbital fissures. The genus is probably referred to the family Goneplacidae H. Milne Edwards, 1852. Withers (1924) reported *Varuna* ? sp. from the Eocene of Jamaica, but that occurrence was based only upon a portion of the merus of the cheliped; therefore, the systematic position of the species is doubtful. Karasawa (1993) described a new species, *Varuna angustifrons*, from the lower Oligocene of Japan; however, the species was moved from *Varuna* to *Carinocarcinoides* Karasawa and Fudouji, 2000 of the family Goneplacidae (Karasawa and Fudouji, 2000).

Fossil records of the Cyclograpsinae comprise three genera, *Cyclograpsus*, *Miosesarma* and *Helice*, all known from the Miocene of Japan (Karasawa, 1989; Karasawa and Inoue, 1992; Karasawa, 1993; Kato, 1996).

The extinct genus *Palaeograpsus* Bittner, 1875 has not been placed within any of the grapsid subfamilies (Glaessner, 1969). Previously known species of the genus include: *Palaeograpsus attenuatus* Bittner, 1875, *P.*



**Table 4.** Distributions and geologic ranges of recognized fossil species of the family Grapsidae.

Taxa	Range	Locality
Family Grapsidae MacLeay, 1838		
Subfamily Grapsinae MacLeay, 1838		
Genus <i>Metopograpsus</i> H. Milne Edwards, 1853		
<i>Metopograpsus traxleri</i> Müller, 1998	L. Miocene	Austria
Genus <i>Pachygrapsus</i> Randall, 1840		
<i>Pachygrapsus hungaricus</i> Müller, 1974	M. Miocene	Hungary, Poland
<i>Pachygrapsus</i> sp., Morris, 1993	Pleistocene	Jamaica
Genus <i>Planes</i> Bowdich, 1825		
<i>Planes prior</i> (Smirnov, 1929)	L. Miocene	Caucasus
Subfamily Sesarinae Dana, 1851		
Genus <i>Sesarma</i> Say, 1917		
<i>Sesarma paraensis</i> Beurlen, 1958	U. Oligo.- L. Mio.	Brazil
<i>Sesarma</i> (s.l.) ? sp., Karasawa, 1993	M. Miocene	Japan
Genus <i>Neosarmatium</i> Sèrene and Soh, 1970		
<i>Neosarmatium smithi</i> (H. Milne Edwards, 1853)	Pleistocene	Australia
Subfamily Cyclograpsinae H. Milne Edwards, 1853		
Genus <i>Cyclograpsus</i> H. Milne Edwards, 1837		
<i>Cyclograpsus directus</i> Karasawa, 1989	L. Miocene	Japan
<i>Cyclograpsus rectangularis</i> Karasawa, 1989	M. Miocene	Japan
Genus <i>Helice</i> De Haan, 1835		
<i>Helice</i> sp., Karasawa and Inoue, 1992	M. Miocene	Japan
Genus <i>Miosesarma</i> Karasawa, 1989		
<i>Miosesarma japonicum</i> Karasawa, 1989	L.- M. Miocene	Japan
<i>Miosesarma naguraense</i> Kato, 1996	M. Miocene	Japan
Subfamily Varuninae H. Milne Edwards, 1853		
Genus <i>Brachynotus</i> De Haan, 1833		
<i>Brachynotus febrarius</i> Müller, 1974	M. Miocene	Hungary
Genus <i>Eriocheir</i> De Haan, 1835		
<i>Eriocheir japonica</i> (De Haan, 1835), Karasawa and Narita, 2000	L. Pliocene	Japan
Genus <i>Hemigrapsus</i> Dana, 1851		
<i>Hemigrapsus oregonensis</i> (Dana, 1851), Rathbun, 1926	Pleistocene	U.S.A.
<i>Hemigrapsus nudus</i> (Dana, 1851), Rathbun, 1926	Pleistocene	U.S.A.
<i>Hemigrapsus</i> sp., Rathbun, 1926	Pleistocene	U.S.A.
Genus <i>Miograpsus</i> Fleming, 1981		
<i>Miograpsus papaka</i> Fleming, 1981	L. Miocene	New Zealand
Genus <i>Varuna</i> H. Milne Edwards, 1830		
<i>Varuna</i> ? sp., Withers, 1924	M. Eocene	Jamaica
Genus <i>Utica</i> White, 1847		
<i>Utica haswelli</i> Wintle, 1886	Pleistocene	Australia
<i>Utica yarraensis</i> Wintle, 1886	Pleistocene	Australia
Subfamily uncertain		
Genus <i>Daragrapsus</i> Müller and Collins, 1991		
<i>Daragrapsus trispinosus</i> Müller and Collins, 1991	U. Eocene	Hungary
Genus <i>Daranyia</i> Lörenthey, 1901		
<i>Daranyia granulata</i> Lörenthey, 1901	U. Eocene	Hungary
<i>Daranyia fabiani</i> Di Salvo, 1933	M. Eocene	Italy
Genus <i>Pseudodaranyia</i> Tessier et al., 1999		
<i>Pseudodaranyia carinata</i> Tessier et al., 1999	M. Eocene	Italy

*bartonensis* Quayle and Collins, 1981, *P. depressus* Quayle and Collins, 1981, *P. guerini* Via, 1959, *P. inflatus* Bittner, 1875 (type species), *P. loczyanus* Lörenthey, 1898 and *P. parvus* Müller and Collins, 1991 from the Eocene of Europe; *P. bittneri* Morris and Collins, 1991 from the Pliocene of Brunei. Among these, Schweitzer and Feldmann (2001) moved three species, *P. bartonensis*, *P. bittneri* and *P. depressus*, to the chasmocarcine genus *Orthakrolophos* Schweitzer and Feldmann, 2001, within the Goneplacidae. *Palaeograpsus guerini* is similar to members of *Orthakrolophos*, but is characterized by having transverse ridges on the dorsal carapace which are lacking in *Orthakrolophos*; therefore, Schweitzer and Feldmann (2001) did not include the species in *Orthakrolophos*. The species remains doubtfully placed within *Palaeograpsus*.

In his original description of the genus, Bittner (1875) indicated that *Palaeograpsus* had a close affinity with *Varuna* and *Pseudograpsus* within the Varuninae. Via (1959) suggested that *P. loczyanus* closely resembles members of *Carcinoplax* H. Milne Edwards, 1852 within the Goneplacidae. Beschin *et al.* (1994) reported well preserved carapaces associated with chelipeds and pereopods of *P. loczyanus*. De Angeli (1995) also described carapaces, abdominal sternites, chelipeds and pereopods of *P. inflatus*, the type species of the genus. We agree with the opinion of Via (1959). Examination of their specimens and the type specimen of *P. loczyanus* by one of us (Karasawa) strongly suggests that *Palaeograpsus* should be placed within the Goneplacidae. In *P. inflatus* and *P. loczyanus* the infraorbital ridge is absent; a median depression on thoracic sternite 3 is present, and a groove between sternites 3 and 4 is deep and well defined. However, in members of the Grapsidae sternite 3 usually lacks a median depression and a well defined groove between sternites 3 and 4 is absent. *Varuna* and *Pseudograpsus* possess the infraorbital ridge which *Palaeograpsus* lacks, a unique character of the Varuninae. *Palaeograpsus inflatus* and *P. loczyanus* have slender meri of the pereopods while genera within the Grapsidae usually possess broad, flattened meri. *Palaeograpsus inflatus* and *P. loczyanus* possess carapace and cheliped characters most like those of *Carcinoplax*. However, the male abdominal somites 3 and 4 of *P. inflatus* are fused, while members of *Carcinoplax* have seven free abdominal somites in males.

The genus *Daranyia* Lörenthey, 1901 was found in the Eocene of Hungary (Lörenthey, 1901; Lörenthey and Beurlen, 1929) and Italy (Di Salvo, 1933). Lörenthey (1901) and Lörenthey and Beurlen (1929) compared *Daranyia* with the extant genus *Euchirograpsus*, but the genus differs from *Euchirograpsus* by having a wide, sinuous frontal margin and well separated anterolateral teeth. Glaessner (1969) did not classify the genus in a known subfamily. We agree with Glaessner's opinion. Only the dorsal carapace of the genus is yet known. The subfamilial arrangement of the genus must await discovery of a ventral carapace and thoracic sternites.

Müller and Collins (1991) erected two monotypic genera, *Daragrapsus* and *Sculptoplax*, within the Grapsidae, based on material from the Hungarian Eocene. *Sculptoplax* does not appear to be a member of the Grapsidae. *Sculptoplax*

resembles the xanthid genus *Carpilodes* Dana, 1851 (= *Liomera* Dana, 1851; ICZN Opinion 73) (Müller and Collins, 1991: 90); therefore, the genus is referred to the Xanthidae s.l. Müller and Collins (1991) indicated that *Daragrapsus* resembled *Daranyia*, but because the genus is represented by only a dorsal carapace specimen, subfamilial placement remains obscure.

Tessier *et al.* (1999) described two new grapsid genera, *Maingrapsus* and *Pseudodaranyia*, from the Eocene of Italy. Although Tessier *et al.* (1999) compared *Maingrapsus* with *Palaeograpsus*, the systematic position of the genus is doubtful. *Maingrapsus* is characterized by having a strongly inflated carapace with three transverse ridges and a wide, anteriorly protruded front, and lacking the infraorbital ridge and anterolateral teeth. There is no similarity between *Maingrapsus* and any known extant members of the Grapsidae. The genus has a resemblance to *Paracorallicarcinus* Tessier *et al.*, 1999, but differs in having a longer carapace without anterolateral teeth. *Paracorallicarcinus* possesses carapace characters like those of the extant *Georgeoplax* Türkay, 1983 of the family Goneplacidae; however, the carapace in *Paracorallicarcinus* is more inflated with weak transverse ridges and bears well defined anterolateral teeth. Therefore, *Maingrapsus* is placed within the family Goneplacidae. The subfamilial placement of *Pseudodaranyia* awaits the discovery of better material.

Thus 25 species in 17 genera of the family Grapsidae are recognized as fossils (Table 4). Three species in three extinct genera are not referred to any known subfamilies. Only the Plagusinae lacks fossil records.

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# Age calibration of megafossil biochronology based on Early Campanian planktonic foraminifera from Hokkaido, Japan

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**Abstract.** The occurrence of an Early Campanian planktonic foraminiferal assemblage consisting of *Globotruncana arca*, *G. linneiana*, *Rosita fornicata* and *R. patelliformis* is first reported from the Upper Haborogawa Formation exposed in the Haboro area, northwestern Hokkaido, Japan. This finding supports the previous interpretation that the Santonian/Campanian boundary can be placed at the basal part of *Inoceramus* (*Platyceramus*) *japonicus* Zone of the inoceramid biostratigraphy.

**Key words:** biostratigraphy, Hokkaido, planktonic foraminifera, Santonian/Campanian boundary

## Introduction

The Late Cretaceous ammonoid and inoceramid zonal schemes in Japan have been progressively improved by several recent biostratigraphic studies (e.g. Toshimitsu and Maiya, 1986; Toshimitsu *et al.*, 1995a, b; Toshimitsu *et al.*, 1998). Five standard inoceramid zones, i.e. *Inoceramus* (*I.*) *uwajimensis*, *I. (I.) mihoensis*, *I. (I.) amakusensis*, *I. (Platyceramus) japonicus* and *Sphenoceramus schmidtii* - *S. orientalis* in ascending order have been proposed by Toshimitsu *et al.* (1995b) for the Coniacian to middle Campanian sequence in the Haboro area, northwestern Hokkaido.

The megafossil assemblages in northwestern Hokkaido, however, lack frequently the Tethyan zonal markers, particularly during the Santonian to Maastrichtian intervals. This scarcity of marker species causes the international correlation difficult between the Tethyan and the Northwestern Pacific bioprovinces including Japan.

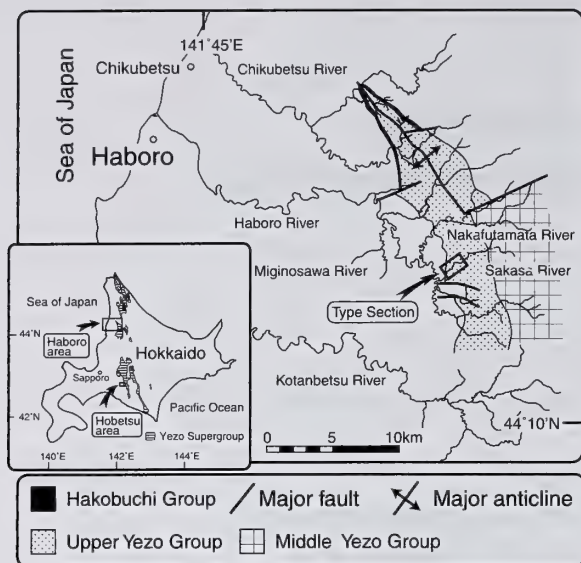
We here report the occurrence of the Tethyan planktonic foraminiferal species *Rosita patelliformis* (Gandolfi) from the Cretaceous Upper Yezo Group in the Haboro area and discuss age calibration of megafossil biochronology.

## Geological setting and lithostratigraphy

The Upper Cretaceous strata exposed in the Haboro area are lithostratigraphically divided into three units, namely the

Middle Yezo, Upper Yezo, and Hakobuchi Groups in ascending order (Figure 1). The Middle Yezo Group is composed of the Shirochi Formation. The Upper Yezo Group is subdivided into the Lower, Middle and Upper Haborogawa Formations. The Hakobuchi Group consists of the Pankezawa Formation. The Shirochi Formation is composed of alternating beds of sandstone and mudstone, and the Lower and Middle Haborogawa Formations consist of mudstone. The Upper Haborogawa Formation is characterized by two coarsening upward sequences, each of which begins with mudstones, graded to bioturbated muddy sandstones and ends with thick-bedded sandstones (Moriya and Hirano, 2001). The Pankezawa Formation is mainly composed of sandstone.

As concerns the Upper Haborogawa Formation in the study area (Figures 1, 2), the thickness of the first sequence is about 550 m, while the second one is approximately about 530 m. The mudstones in the lower part of the first sequence are intercalated with 4 to 5 cm thick, medium-bedded, fine- to medium-grained sandstones (Figure 3). The sandstone intercalations tend to be more frequent toward the top of the sequence. The uppermost part of the sequence represents a 10 m thick sandstone unit, named UHs1 (Toshimitsu, 1985), which is pale-green-colored, parallel- and cross-laminated, frequently interbedded with thin mudstone of a few cm thick (Figure 3). This unit can be traced laterally as a marker horizon in the investigated area (Figure 2). The weakly laminated mudstones of the second

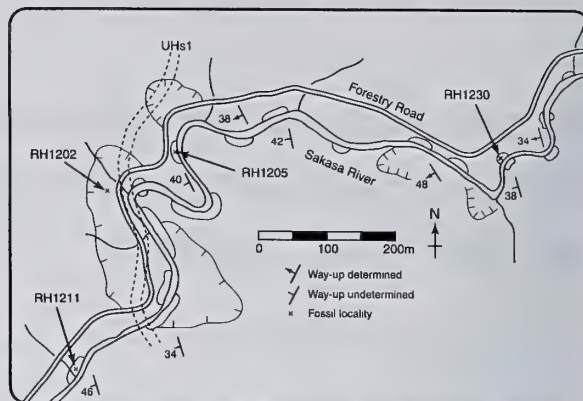


**Figure 1.** Index map and geological outline of the study area. The rectangle shows the investigated area where the type section of the Upper Haborogawa Formation is exposed.

cycle overlies the unit UHs1, but the upper part of this cycle is not exposed in the investigated section (Figures 2, 3).

### Material and methods

We collected three sediment samples from mudstones or sandy mudstones of the upper part of the Upper Haborogawa Formation at locs. RH1202 (along the Sakasagawa Forestry Road in the Haboro area), RH2530 and



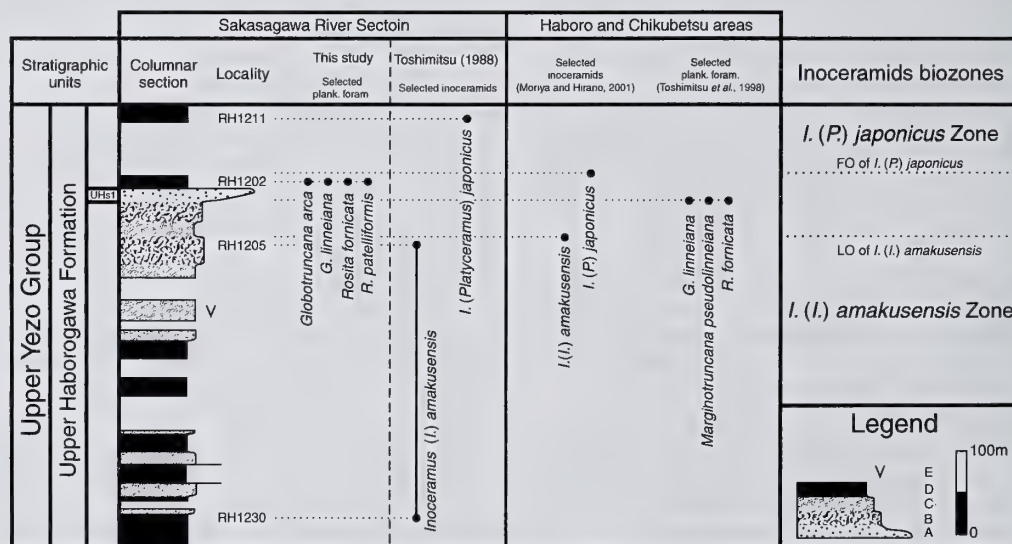
**Figure 2.** Route map of the type section of the Upper Haborogawa Formation along the Sakasa River in the Haboro area, showing the mega- and microfossil localities. For RH numbers, refer Toshimitsu (1985).

RH2531 (along the Nakafutamata River) (for RH1202 refer Figures 2, 3; for RH2530 and 2531 refer Toshimitsu, 1985, fig. 5a).

In a laboratory, each sample, 1.5 kg in weight was disaggregated with hydrogen peroxide and sodium tetraphenylborate (Hanken, 1979) to extract foraminiferal specimens. The disaggregated residues were washed using 75  $\mu$ m sieve. All specimens larger than 125  $\mu$ m were identified. The illustrated planktonic foraminifera (Figure 4) yielded from loc. RH1202 are housed in the University Museum of the University of Tokyo (UMUT).

### Planktonic foraminiferal assemblages

The following species were recognized from the upper



**Figure 3.** Biostratigraphic summary of selected mega- and microfossils in the Upper Haborogawa Formation along the Sakasagawa River and adjacent areas. The stratigraphic horizons of bioevents are compiled from Toshimitsu (1988), Toshimitsu *et al.* (1998) and Moriya and Hirano (2001; Chikubetsu area). A, sandstone; B, muddy sandstone; C, sandy mudstone; D, mudstone; E, acidic tuff.



**Table 1.** List and the number of specimens of the planktonic foraminiferal specimens occurred from the upper part of the Upper Haborogawa Formation. For the localities of RH2530 and RH2531, see Toshimitsu (1985, fig. 5a).

Species	Locality		
	RH 2531	RH 2530	RH 1202
<i>Archaeoglobigerina blowi</i>		17	
<i>A. bosquensis</i>		14	
<i>A. cretacea</i>		8	1
<i>Dicarinella</i> sp.		3	
<i>Globigerinelloides asper</i>		3	
<i>Globotruncana arca</i>		6	4
<i>Globo. cf. arca</i>		10	
<i>Globo. bulloides</i>		40	15
<i>Globo. lapparenti</i>			1
<i>Globo. linneiana</i>	16	125	38
<i>Hedbergella</i> aff. <i>planispira</i>	1		
<i>Heterohelix reussi</i>		1	
<i>Marginotruncana pseudolinneiana</i>	1	9	
<i>Rosita fornicata</i>		8	1
<i>Rosita patelliformis</i>			1

part of the Upper Haborogawa Formation: *Archaeoglobigerina blowi* Pessagno, *A. bosquensis* Pessagno, *A. cretacea* (d'Orbigny), *Dicarinella* sp., *Globigerinelloides asper* (Ehrenberg), *Globotruncana arca* (Cushman), *Globo. bulloides* Vogler, *Globo. lapparenti* Brotzen, *Globo. linneiana* (d'Orbigny), *Hedbergella* aff. *planispira* (Tappan), *Heterohelix reussi* (Cushman), *Marginotruncana pseudolinneiana* Pessagno, *Rosita fornicata* (Plummer), and *R. patelliformis* (Table 1). In the assemblages, *Globotruncana linneiana* is the most abundant species at all localities, and *Globotruncana bulloides* is subordinate at locs. RH1202 and 2530. The mudstone sample from loc. RH1202 yielded a total of 61 well-preserved specimens of planktonic foraminifers. Some of them identified as *Globotruncana arca*, *G. linneiana*, *Rosita fornicata*, and *R. patelliformis*, are shown in Figure 4. Among the assemblage, *R. patelliformis* is represented by a single specimen (Table 1), but this is the first report of the species from Japan. This specimen is not so large, having a circular peripheral outline and less convex spiral (Figure 4.1). Although the last chamber is somewhat deformed, chambers in the final whorl are crescentic and narrow, and the surface of the test is not so undulated. Judging from these characters, the specimen is undoubtedly identified as *R. patelliformis*.

### Correlation

Sliter (1989) proposed a scheme of Cretaceous planktonic foraminiferal biostratigraphy, showing the stratigraphic ranges of selected species. The planktonic foraminiferal zonation applied here is based on that study. The first occurrence (FO) of *R. fornicata* is placed closed to the Coniacian/Santonian boundary. Although there are a few objections for the age of FO of *Globotruncana arca* (Kopaevich and Salaj in Hancock and Gale, 1996), *G. arca*

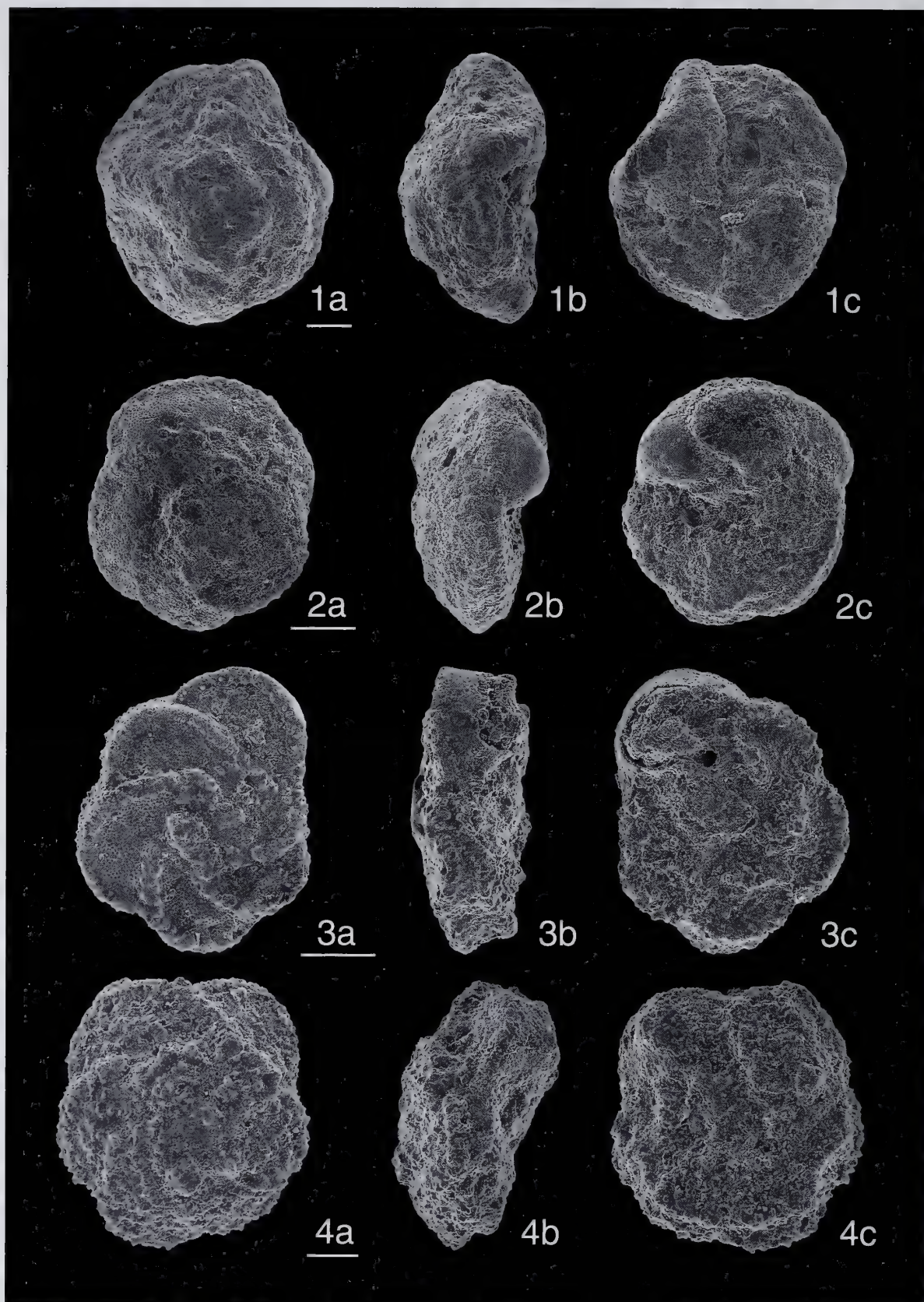
and *G. linneiana* should appear within the uppermost Santonian *Dicarinella asymetrica* Zone (Caron, 1985; Sliter, 1989). The FO of *R. patelliformis* is placed within the *Globotruncana elevata* Zone of the upper part of the Lower Campanian. The assemblage from the mudstone sample at loc. RH1202 is, therefore, assigned an age of Early Campanian, probably the *G. elevata* Zone.

### Discussion

*Inoceramus* (*Inoceramus*) *amakusensis* Nagao and Matsumoto was obtained from bioturbated muddy sandstones at locs. RH1205 and RH1230 (Toshimitsu, 1985; Figures 2, 3). *I. (Platyceramus) japonicus* Nagao and Matsumoto occurs from the mudstones above the UHs1 sandstones (Toshimitsu, 1988; loc. RH 1211 in Figures 2, 3). The last occurrence (LO) of *I. (I.) amakusensis* is recognized at about 50 m below the unit UHs1, whereas *I. (P.) japonicus* first appears at about 20 m above UHs1 (Toshimitsu, 1998; Moriya and Hirano, 2001). Hence, the Upper Haborogawa Formation can be biostratigraphically divided into the *I. (I.) amakusensis* and *I. (P.) japonicus* Zones, with a boundary within the UHs1 sandstones (Figure 3).

Toshimitsu *et al.* (1998) defined the Santonian/Campanian boundary by the FOs of the ammonoid *Submorticeras* cf. *condamyi* (Collignon) and a planktonic foraminifer *Globotruncana arca* in the Haboro area, and placed the boundary just above the UHs1 of the Upper Haborogawa Formation.

Hancock (1991) initially stated that the FO of *Submorticeras* might coincide with the Santonian/Campanian boundary. The evolution of *Submorticeras* from *Texanites* was, however, later inferred to have occurred during the late Santonian (Gale *et al.*, 1995; Hancock and Gale, 1996). Furthermore, although Kopaevich and Salaj (*in* Hancock and





Gale, 1996) emphasized that the "G. arca" which occurred from the Upper Santonian is an ancestral form of the true "G. arca", the FO of G. arca should be placed within the upper Santonian D. asymetrica Zone (e.g., Caron, 1985; Sliter, 1989; Hancock and Gale, 1996). Therefore, the FOs of Submortoniceras and G. arca are inappropriate as the boundary markers, and these bioevents have not been adopted as Santonian/Campanian boundary criteria (Hancock and Gale, 1996).

We found an Early Campanian planktonic foraminiferal assemblage consisting of Globotruncana arca, G. linneiana, Rosita formicata and R. patelliformis from just above the unit UHs1 of the upper part of the Upper Haborogawa Formation in the Haboro area (Figures 2, 33; loc. RH1202 along the Sakasagawa Forestry Road in the Haboro area). Toshimitsu et al. (1998) found a Late Santonian planktonic foraminiferal assemblage consisting of Globotruncana linneiana, Marginotruncana pseudolinneiana and Rosita formicata from mudstones just below the UHs1 unit along the Miginosawa Creek. Toshimitsu et al. (1998) also described the occurrence of Globigerinelloides prairiehillensis Pessagno from about 200 m above the UHs1 unit along the Kotanbetsu River. Therefore, in the Haboro area, the Santonian/Campanian boundary can be temporally placed at the top of the unit UHs1.

This level is very close to the boundary between the Inoceramus (I.) amakusensis Zone and the I. (Platyceramus) japonicus Zone of the inoceramid biostratigraphy (Figure 3). Toshimitsu et al. (1998) expected to place the Santonian/Campanian boundary at the basal part of the I. (P.) japonicus Zone and our finding substantiates this idea.

The K-Ar dating, furthermore, revealed that in the Horosari-zawa section of the Hobetsu area, a white acid tuff intercalated with mudstones of the lower part of the I. (P.) japonicus Zone is dated at  $82.2 \pm 0.6$  Ma (Shibata and Uchiumi, 1995; Toshimitsu et al., 1998). The K-Ar age supports the idea that the age of the I. (P.) japonicus Zone is Early Campanian.

### Concluding remarks

In this paper, we have reported the FO of Rosita patelliformis at about 10 m above the sandstone beds UHs1 (Figures 2, 3; loc. RH1202 along the Sakasagawa Forestry Road in the Haboro area). Our new finding of this planktonic foraminifera suggests that the Santonian/Campanian boundary should be drawn around the horizon of the sandstone beds UHs1, probably close to the boundary between the I. amakusensis and I. (P.) japonicus Zones as proposed by Toshimitsu et al. (1998).

Hancock and Gale (1996) proposed the following Santonian/Campanian boundary criteria: (1) the lowest occurrence of the ammonoid Placenticeras bidorsatum (Roemer), (2) the extinction level of the crinoid Marsupites

testudinarius (Schlotheim), (3) the extinction in the planktonic foraminifers of Dicarinella concavata group, (4) the first occurrence (FO) of nannofossil Broinsonia parca (Stradner), and (5) the basal part of the paleomagnetic the Chron C33r. To set the Santonian/Campanian boundary precisely in Japan, we need to inspect these boundary criteria for further study.

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➡ **Figure 4.** Planktonic foraminifera from the loc. RH1202 along the Sakasagawa forestry road in the Haboro area. **1a-c.** *Rosita patelliformis* (Gandolfi), UMUT MF 27977. **2a-c.** *Rosita formicata* (Plummer), UMUT MF 27978. **3a-c.** *Globotruncana linneiana* (d'Orbigny), UMUT MF 27979. **4a-c.** *Globotruncana arca* Cushman, UMUT MF 27980. 1-3, Scale bars are 100  $\mu$ m; 4, Scale bar is 50  $\mu$ m.

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## Middle Permian brachiopods from the Moribu area, Hida Gaien Belt, central Japan

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**Abstract.** A Middle Permian (Murgabian) brachiopod fauna is described from the lower Moribu Formation in the Moribu area, Hida Gaien Belt, central Japan. This fauna consists of 29 species, of which 2 are new, in 27 genera. The new species are *Fallaxoproductus moribuensis* and *Alispiriferella japonica*. The Moribu fauna is a Boreal-Tethyan mixed fauna and allied with the Middle Permian brachiopod faunas of central Japan (Ise in the Hida Gaien Belt), northeast Japan (South Kitakami Belt), eastern Russia (South Primorye), northeast China (Jilin) and north China (Inner Mongolia). These regions were probably a continental shelf bordering the northeastern margin of the Sino-Korean block, which was present at a middle northern palaeolatitude in the Middle Permian time.

**Key words:** Boreal-Tethyan mixed fauna, brachiopods, Hida Gaien Belt, Middle Permian, Moribu

### Introduction

The brachiopod fauna that is the subject of this paper was recovered from the lower member of the Moribu Formation in the Moribu area, about 10 km NE of Takayama, Hida Gaien Belt, central Japan (Figure 1). The Moribu Formation was named by Isomi and Nozawa (1957) for a Permian succession of the Hongo-Arakigawa area including the Moribu area. Since then the stratigraphy of the Moribu Formation has been discussed by Fujimoto *et al.* (1962), Yamada and Yamano (1980), Horikoshi *et al.* (1987), Tanase and Kasahara (1988), Tazawa (1996), and Yoshida and Tazawa (2000).

Faunal data for the Moribu Formation are included in several papers, fusulinaceans by Yamada and Yamano (1980) and Tazawa *et al.* (1993), radiolarians by Umeda and Ezaki (1997), corals by Yamada and Yamano (1980), and brachiopods by Horikoshi *et al.* (1987), Tazawa (1999a, b), and Shi and Tazawa (2001). To date, 5 fusulinacean and 3 brachiopod species have been described. Permian brachiopods of the Hida Gaien Belt are poorly known. Only one fauna, consisting of 13 species in 12 genera, was described by Tazawa and Matsumoto (1998) from the Oguradani Formation in the Ise area, about 80 km SW of Moribu. Thus, the Moribu fauna is the second-described but more plentiful Permian brachiopod fauna in the Hida Gaien Belt.

The purpose of the present study is to describe all available brachiopod elements of the Moribu fauna, and to discuss the age and palaeobiogeography of this fauna. The brachiopod fossils were collected from 10 localities in the

Moribu area by E. Horikoshi (and his students), K. Tsushima, Y. Miyake and by myself in 1985–1999. All specimens described in this paper are housed in the Department of Geology, Faculty of Science, Niigata University.

### Stratigraphy

Fossil localities, geological map and columnar sections of the Moribu Formation are shown in Figures 2–4, respectively. The Moribu Formation is distributed in the northwestern part of the Moribu area, having a general trend of NE–SW, and dipping towards the NW, although there are beds striking N–S or NW–SE and dipping W to SW in the eastern part. The Moribu Formation is composed of shallow marine continental shelf sediments and lithologically subdivided into three members, the lower shale-sandstone member (550 m thick) with some conglomerate and limestone beds, the middle sandstone member (230 m thick) with some tuffaceous sandstone beds, and the upper shale member (more than 650 m thick) with numerous, thin sandstone layers. The total thickness of this formation is more than 1,430 m. The Moribu Formation covers the Lower to Upper Carboniferous Arakigawa Formation with an unconformity, and is in turn unconformably overlain by the Upper Cretaceous–Palaeogene volcanic rocks (Nohi rhyolites). In general the Moribu Formation is sparsely fossiliferous. The lower member contains various marine invertebrate fossils, such as fusulinaceans, corals, bryozoans, brachiopods, bivalves, gastropods and crinoids. The middle member lacks macrofossils, but

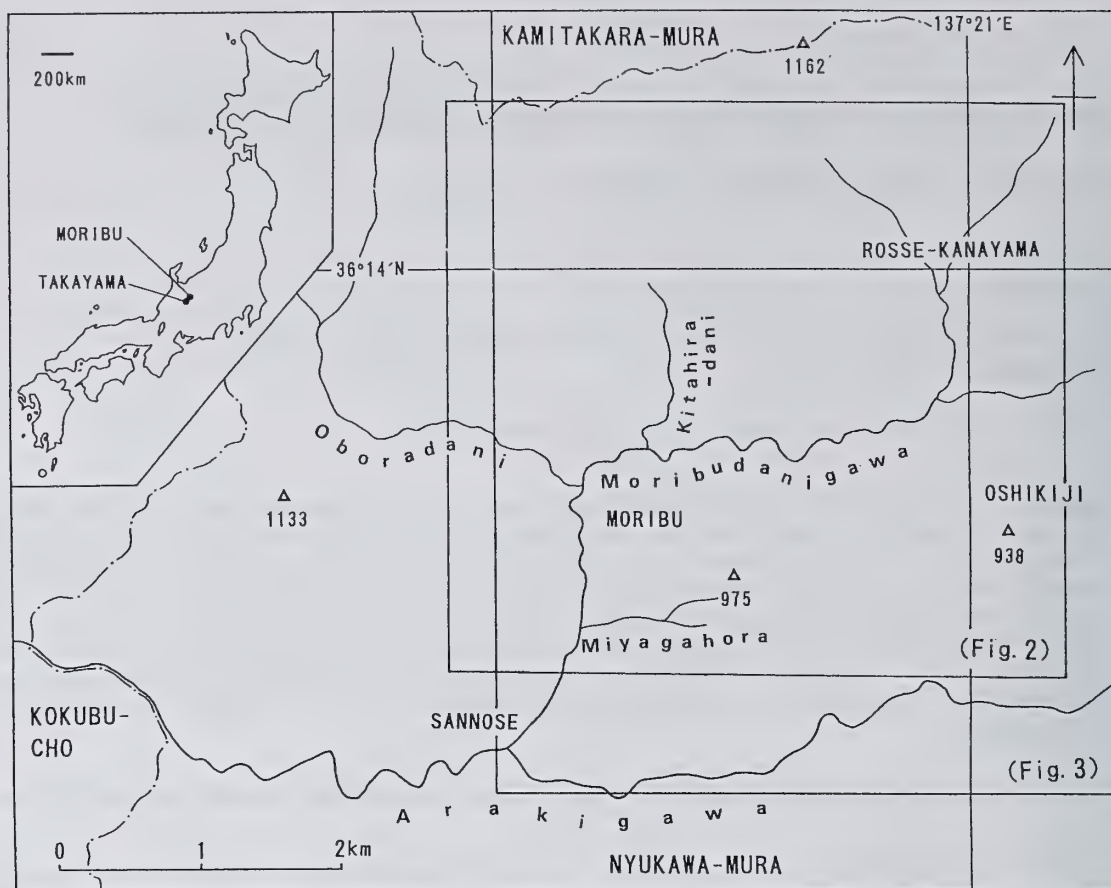


Figure 1. Index map showing the study area.

contains fusulinaceans and radiolarians in some horizons. The upper member is barren of fossils.

Brachiopods are the most common macrofossils. The brachiopod fossils treated in this paper were collected from the shale, sandstone and argillaceous impure limestone of the lower member at 10 localities (HMF1, 2, 3, 5, 8, 12, 13, 14, 16 and 25) (Figure 2). The topographical and stratigraphical positions, rock types and brachiopod lists of the collecting localities are as follows (see also Figure 4):

HMF1: Black shale, 10 m below the limestone of the lower member, at the left (east) bank of the lower Moribudanigawa River, 200 m S of a bridge in Moribu Village (Lat.  $36^{\circ}12'41''$  N, Long.  $137^{\circ}19'10''$  E); *Enteleles* sp., *Rhynchopora* sp., *Hustedia ratburiensis* Waterhouse and Piyasin, *Martiniopsis* sp., *Blaspirifer* cf. *reedi* (Licharew), and *Alispiriferella japonica* sp. nov.

HMF2: Dark grey argillaceous impure limestone, 4 m above the base of the limestone of the lower member, at the right (west) bank of the lower Moribudanigawa River, 30 m SW of HMF1; *Capillomesolobus* sp., *Transennatia gratiosa* (Waagen), *Reticulatia* sp., *Linoproductus lineatus* (Waagen), *Megousia* sp., *Cancrinella* cf. *spinosa* Hayasaka and Minato, *Urushtenoidea crenulata* (Ting), *Leptodus nobilis* (Waagen),

*Derbyia* sp., *Stenosisma margaritovi* (Tschernyschew), *Hustedia ratburiensis* Waterhouse and Piyasin, *Spiriferella lita* (Fredericks), and *Alispiriferella japonica* sp. nov.

HMF3: Black shale, 10 m above the calcareous conglomerate of the lower member, at the left bank of the middle Moribudanigawa River, 130 m W of the junction of the Kuragatani Valley and the Moribudanigawa River (Lat.  $36^{\circ}13'24''$  N, Long.  $137^{\circ}20'42''$  E); *Orbiculoidea* cf. *jangarensis* Ustritsky, *Stenosisma margaritovi* (Tschernyschew), *Hustedia ratburiensis* Waterhouse and Piyasin, *Martinia* sp., *Blaspirifer* cf. *reedi* (Licharew), and *Dielasma* sp.

HMF5: Grey fine-grained sandstone, 65 m below the sandstone of the middle member, at the left bank of the upper Moribudanigawa River, 250 m NW of the junction of the Suganotani Valley and the Moribudanigawa River (Lat.  $36^{\circ}14'17''$  N, Long.  $137^{\circ}20'29''$  E); *Yakovlevia kaluzinensis* Fredericks, *Juresania* cf. *juresanensis* (Tschernyschew), *Hustedia ratburiensis* Waterhouse and Piyasin, *Gypospirifer volatilis* Duan and Li, and *Alispiriferella japonica* sp. nov.

HMF8: Black shale, 20 m below the limestone of the lower member, at 75 m upper from the entrance of a small tributary in the middle Moribudanigawa River, 250 m NE of HMF12; *Linoproductus lineatus* (Waagen), *Neospirifer* cf. *fasciger* (Keyserling), and *Alispiriferella japonica* sp. nov.



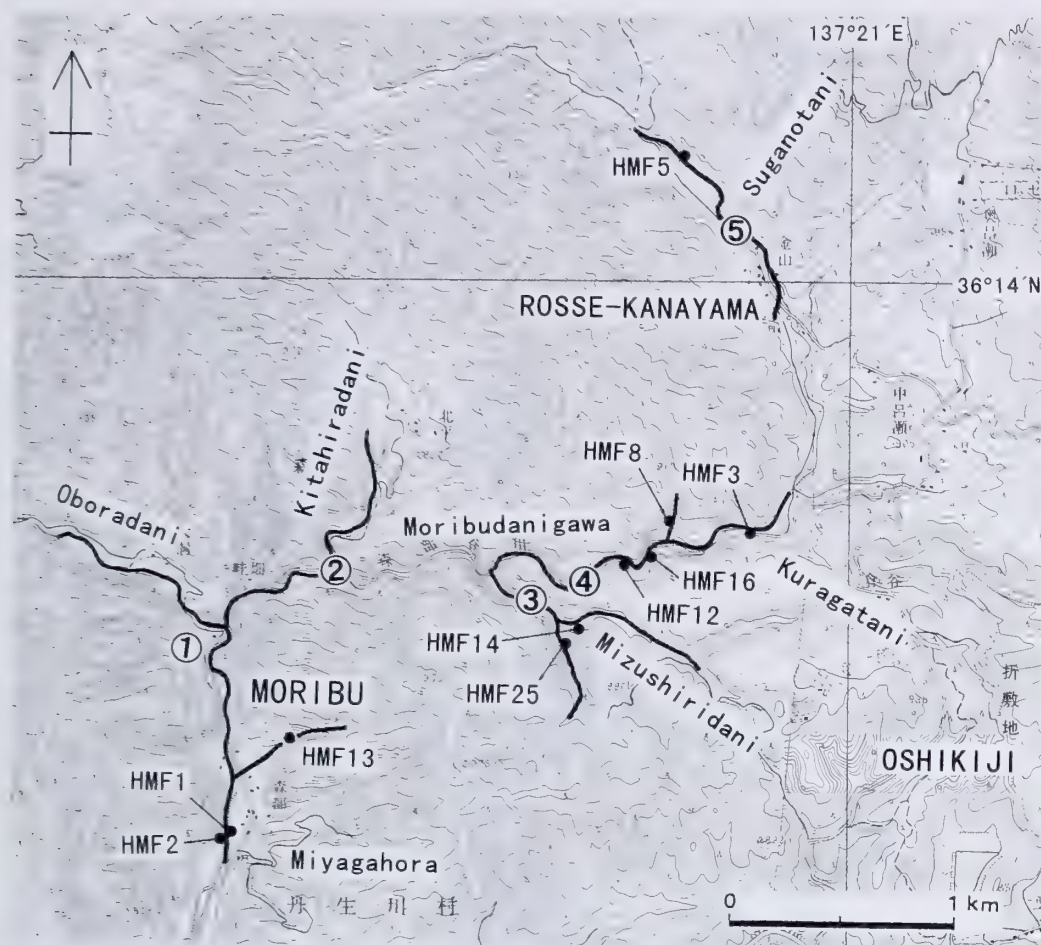


Figure 2. Index map showing the fossil localities (HMF1-3, 5, 8, 12-14, 16, 25) and the studied sections (①-⑤).

HMF12: Black shale, 5 m below the limestone of the lower member, at the left (south) bank of the middle Moribudanigawa River, 625 m E of the junction of the Mizuyagadani Valley and the Moribudanigawa River (Lat. 36° 13' 20" N, Long. 137° 20' 21" E); *Yakovlevia kaluzinensis* Fredericks, *Waagenoconcha permocarbonica* Ustritsky, *Waagenoconcha* cf. *imperfecta* Prendergast, *Fallaxoproductus moribuensis* sp. nov., *Permudaria asiatica* Nakamura, Kato and Choi, *Gypospirifer volatilis* Duan and Li, and *Alispiriferella ordinaria* (Einar).

HMF13: Black shale of the same horizon as HMF1, at the eastern slope facing the lower Moribudanigawa River, 500 m NNE of HMF1; *Transennatia gratiosa* (Waagen).

HMF14: Black shale, 10 m below the limestone of the lower member, at the middle Mizushiridani Valley, 500 m SE of the junction of the Mizushiridani Valley and the Moribudanigawa River (Lat. 36° 13' 10" N, Long. 137° 20' 12" E); *Yakovlevia kaluzinensis* Fredericks and *Alispiriferella japonica* sp. nov.

HMF16: Black shale of the same horizon of HMF8, at the left (east) bank of the middle Moribudanigawa River, 125 m NE of HMF12; *Alispiriferella japonica* sp. nov.

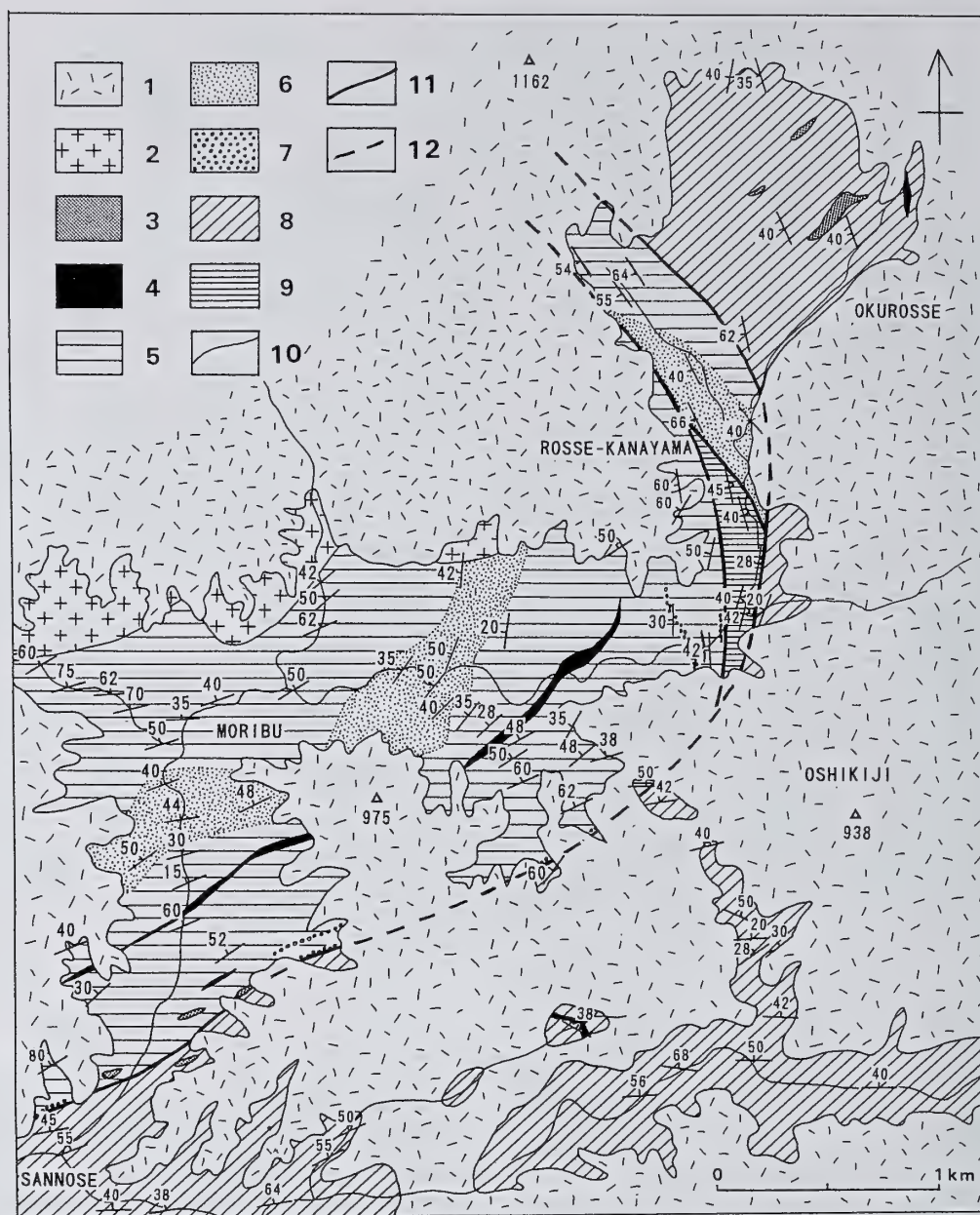
HMF25: Black shale, 30m below the limestone of the lower member, at 100 m SW of HMF14; *Yakovlevia kaluzinensis* Fredericks and *Gypospirifer volatilis* Duan and Li.

### The Moribu fauna

#### Age and Correlation

The brachiopod fauna described here includes the following 29 species assigned to 27 genera: *Orbiculoidea* cf. *jangarensis* Ustritsky, *Capillomesolobus* sp., *Transennatia gratiosa* (Waagen), *Yakovlevia kaluzinensis* Fredericks, *Reticulatia* sp., *Juresania* cf. *juresanensis* (Tschernyschew), *Waagenoconcha permocarbonica* Ustritsky, *Waagenoconcha* cf. *imperfecta* Prendergast, *Linoproductus lineatus* (Waagen), *Megousia* sp., *Cancrinella* cf. *spinosa* Hayasaka and Minato, *Fallaxoproductus moribuensis* sp. nov., *Permudaria asiatica* Nakamura, Kato and Choi, *Urushtenoidea crenulata* (Ting), *Leptodus nobilis* (Waagen), *Derbyia* sp., *Enteleles* sp., *Stenosisma margaritovi* (Tschernyschew), *Rhynchopora* sp., *Hustedia ratburiensis* Waterhouse and Piyasin, *Martinia* sp., *Martiniopsis* sp., *Neospirifer* cf. *fasciger* (Keyserling), *Blasispirifer* cf. *reedii* (Licharew), *Gypospirifer volatilis* Duan and Li, *Spiriferella lita* (Fredericks), *Alispiriferella ordinaria* (Einar), *Alispiriferella japonica* sp. nov. and *Dielasma* sp.

The list suggests a Middle Permian age, and certain taxa further suggest a narrower age ranging from the Murgabian



**Figure 3.** Geological map of the Moribu area (after Tazawa, Hasegawa and Yoshida, 2000). 1: Late Cretaceous and Palaeogene volcanic rocks, 2: Jurassic granitic rocks, 3: Dyke rocks, 4: Limestone of the Arakigawa and Moribu Formations, 5: Shale-dominant facies of the Moribu Formation, 6: Sandstone of the Moribu Formation, 7: Conglomerate of the Moribu Formation, 8: Arakigawa Formation (Carboniferous), 9: Rosse Formation (Devonian), 10: Unconformity, 11: Fault, 12: Concealed fault.

to the Midian. *Gypospirifer volatilis* has been known only from the Murgabian of Inner Mongolia. *Cancrinella* cf. *spinosa*, *Rhynchopora* sp. and *Blasispirifer* cf. *reedi* are similar to the Murgabian species. *Permudaria asiatica*, *Urushtenoidea crenulata*, *Stenosisma margaritovi* and *Spiriferella lita* are elsewhere known from the Murgabian-Midian. *Yakovlevia kaluzinensis* is known from the Kubergandian-Midian. *Transennatia gratiosa* occurs in the

Murgabian-Dzhulfian. *Waagenoconcha permocarbonica* has a long range from the Middle Carboniferous to the Middle Permian, but the lineage is restricted up to the Murgabian. *Linoproductus lineatus* is a long ranging species from the Middle Carboniferous to the Upper Permian, but most common in the Middle Permian. *Leptodus nobilis* ranges into the Kubergandian-Dorashamian. *Hustedia ratburiensis* is recorded from the Yakhtashian-Dzhulfian.



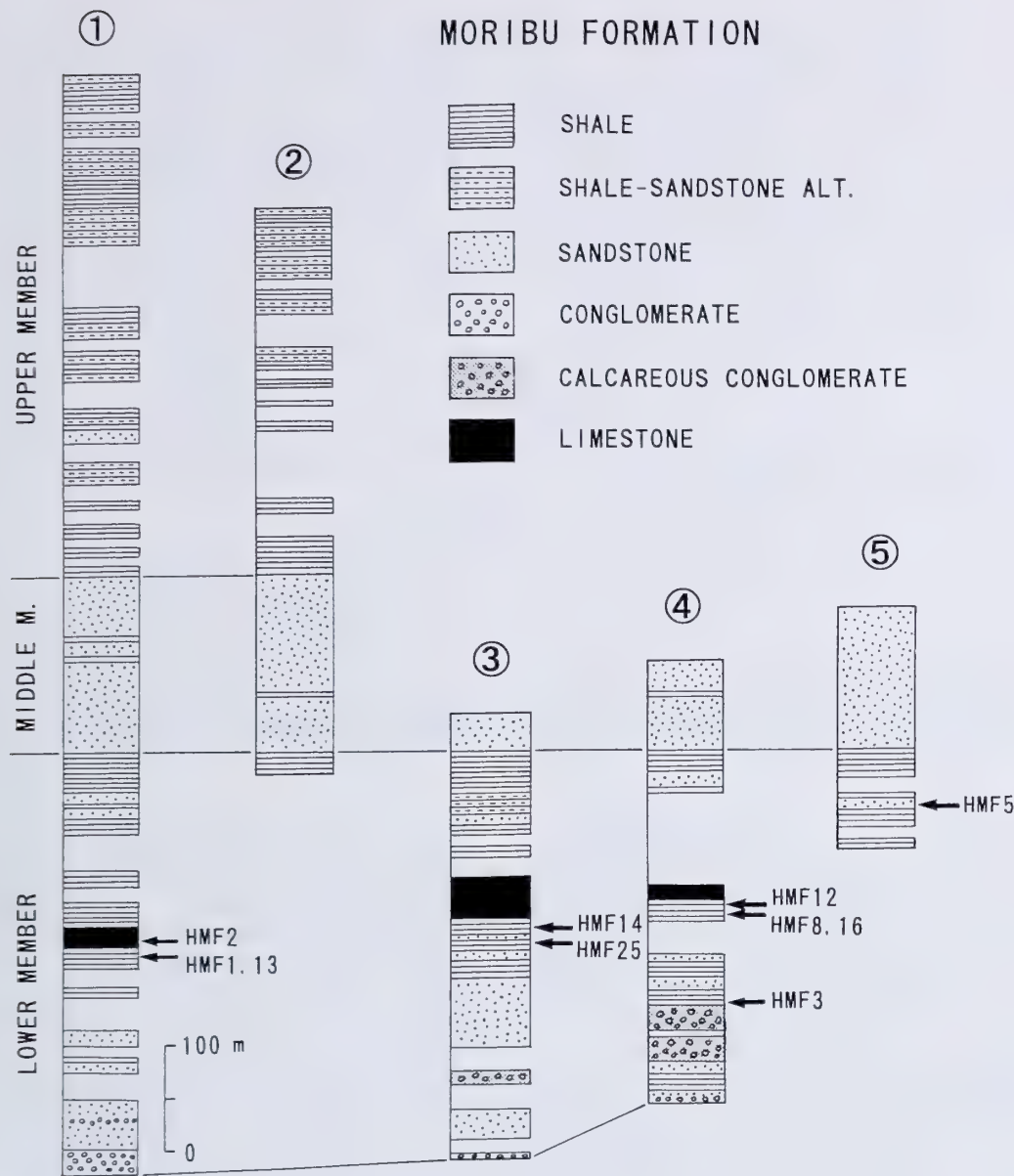


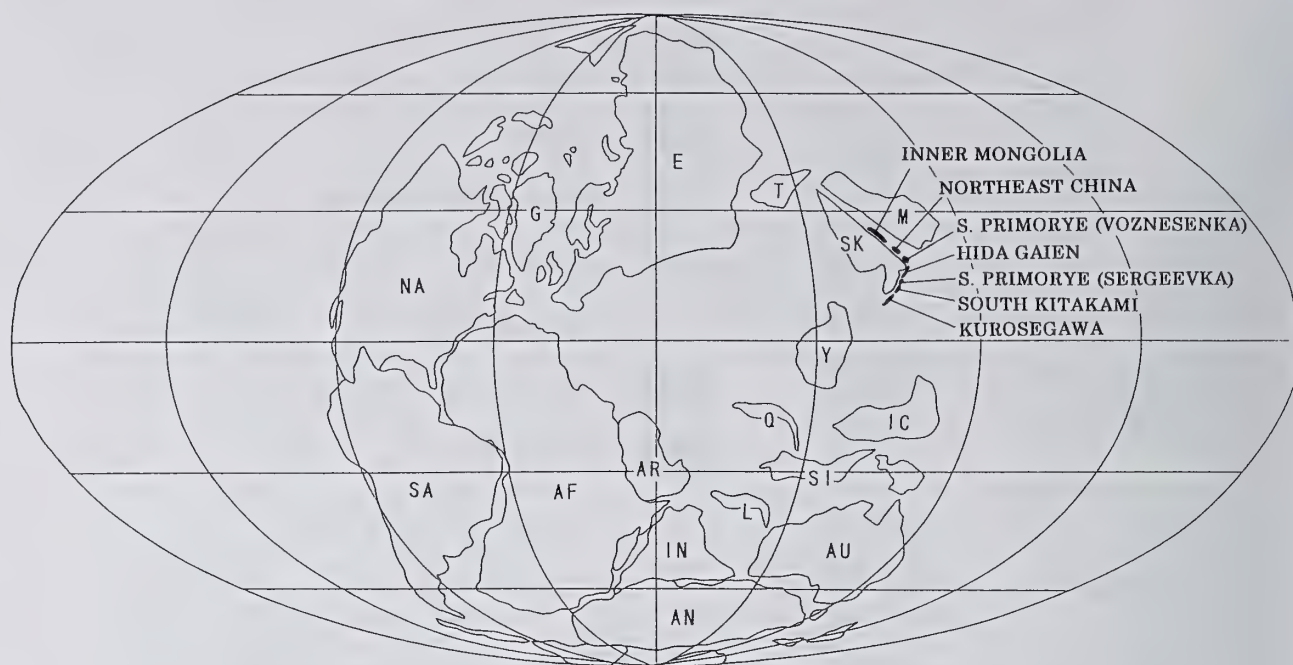
Figure 4. Columnar sections of the Moribu Formation, showing the stratigraphic positions of the fossil localities (HMF1-3, 5, 8, 12-14, 16, 25).

From this evidence, the Moribu fauna can be regarded as Murgabian in age. The Murgabian age assignment does not conflict with data from other fossils of the Moribu Formation.

Published data on fusulinaceans indicate similar age to that shown by brachiopods. The brachiopods occur from the middle and upper parts of the lower member of the Moribu Formation, i.e., the horizons between the calcareous conglomerate of the lower member, with *Pseudofusulina fusiformis* (Schellwien and Dyhrenfurth) and *Misellina* sp., described by Yamada and Yamano (1980), and the sandstone of the middle member, with *Monodioxodina* cf.

*matsubaishi* (Fujimoto), described by Tazawa *et al.* (1993). These fusulinaceans confine the age of the brachiopod fauna between the Kubergandian and Murgabian. Consequently the age of the Moribu fauna is judged to be the Murgabian.

In generic and specific composition, the Moribu fauna is most similar to the Middle Permian brachiopod faunas from the Oguradani Formation of the Ise area, Hida Gaien Belt, central Japan (Tazawa and Matsumoto, 1998), and the Barabash and Chandalaz Formations of South Primorye, eastern Russia (Fredericks, 1924, 1925; Licharew and Kotlyar, 1978; Koczyrkevich, 1979a, b). Furthermore, the



**Figure 5.** Palaeogeographical map in the Middle Permian time (adapted from Ziegler *et al.*, 1996). Black areas are continental shelf. AF: Africa, AN: Antarctica, AR: Arabia, AU: Australia, E: Eurasia, G: Greenland, IC: Indochina, IN: India, L: Lhasa, M: Mongolia, NA: North America, Q: Qiangtang, SA: South America, SI: Sibumasu, SK: Sino-Korea, T: Tarim, Y: Yangtze.

Middle Permian brachiopod faunas from the South Kitakami Belt (Hayasaka, 1925, 1960; Hayasaka and Minato, 1956; Nakamura *et al.*, 1970; Nakamura, 1979; Tazawa, 1979; Tazawa *et al.*, 2000), Jilin, northeast China (Lee *et al.*, 1980) and Inner Mongolia, north China (Grabau, 1931; Lee and Gu, 1976; Lee *et al.*, 1982; Duan and Li, 1985) also closely resembles the Moribu fauna in species composition.

#### Palaeobiogeography of the fauna

Palaeobiogeographically, the Moribu fauna contains rather numerous Boreal or bipolar (anti-tropical) elements, *Yakovlevia kaluzinensis*, *Waagenoconcha permocarbonica*, *Waagenoconcha cf. imperfecta*, *Megousia* sp., *Cancrinella cf. spinosa*, *Fallaxoproductus moribuensis*, *Stenosisma margaritovi*, *Rhynchopora* sp., *Hustedia ratburiensis*, *Blasispirifer cf. reedi*, *Gypospirifer volatilis*, *Spiriferella lita*, *Alispiriferella ordinaria*, and *Alispiriferella japonica*. The Tethyan elements are also present but not abundant in this fauna. The Tethyan-type species in this fauna are *Transennatia gratiosa*, *Permudaria asiatica*, *Urushtenoidea crenulata*, *Leptodus nobilis*, and *Enteletes* sp. Consequently, the Moribu fauna is a mixture of the Boreal (bipolar or anti-tropical) and Tethyan elements, although the Boreal elements are predominant.

The Hida Gaien Belt with the Moribu fauna is restricted geographically to a continental shelf in the transitional zone between the Boreal and Tethyan Realms in east Asia, i.e., the Inner Mongolian-Japanese Transition Zone of Tazawa (1991, 1998), which includes Inner Mongolia, northeast China, South Primorye, Hida Gaien and South Kitakami, and

placed on the northeastern margin of the Sino-Korean block in the middle palaeolatitude of the Northern Hemisphere during the Permian (Figure 5). The Hida Gaien Belt was probably located between the Voznesenka Belt (Barabash-Vladivostok area) and the Sergeevka Belt (Nakhodka-Paltizansk area), and more northerly than the South Kitakami, as mentioned by Tazawa (2001).

#### Systematic descriptions

Order Lingulida Waagen, 1885  
Superfamily Discinoidea Gray, 1840  
Family Discinidae Gray, 1840  
Genus ***Orbiculoidea*** d'Orbigny, 1847

*Type species.*—*Orbicula forbesii* Davidson, 1848.

***Orbiculoidea cf. jangarensis*** Ustritsky, 1960

Figure 6.11

*Compare.*—

*Orbiculoidea jangarensis* Ustritsky, 1960, p. 98, pl. 1, figs. 10–12; Ustritsky and Tschernjak, 1963, p. 68, pl. 1, figs. 5–9; Ifanova, 1972, p. 84, pl. 1, figs. 26–27; Kalashnikov, 1983, p. 204, pl. 45, figs. 3, 4; Kalashnikov, 1993, p. 14, pl. 2, fig. 13; pl. 3, figs. 5a, b; pl. 4, figs. 3a, b.

*Material.*—One specimen, from locality HMF3, external mould of a ventral valve, NU-B370.



**Remarks.**—This specimen is assigned to the genus *Orbiculoidea* due to its elliptical outline, short pedicle opening (7 mm long) and numerous, fine concentric lirae on the ventral valve. The Moribu species is a large *Orbiculoidea* of about 30 mm in diameter, and most resembles *Orbiculoidea jangarensis* Ustritsky, 1960, originally described by Ustritsky (1960) from the Talatin Formation of Pay Khoy, Pechora Basin, northern Russia in size and external ornament. *O. jangarensis* has been known from the Upper Artinskian to the Ufimian of the Pechora Basin and Taimyr Peninsula (Ustritsky, 1960; Ustritsky and Tschernjak, 1963; Ifanova, 1972; Kalashnikov, 1983, 1993).

*Orbiculoidea* sp. Hayasaka (1963, p. 479, figs. 1a, b), from the lower Kanokura Formation of the southern Kitakami Mountains (South Kitakami Belt), northeast Japan, is also close to the present species in size and external ornament of the ventral valve. But accurate comparison is difficult for the fragmentary specimen.

Order Productida Sarytcheva and Sokolskaya, 1959  
Suborder Chonetidina Muir-Wood, 1955  
Superfamily Chonetoidea Bronn, 1862  
Family Rugosochonetidae Muir-Wood, 1962  
Subfamily Capillomesolobinae Pecar, 1986  
Genus *Capillomesolobus* Pecar, 1986

**Type species.**—*Capillomesolobus karavankensis* Pecar, 1986.

### *Capillomesolobus* sp.

Figure 6.8a-6.10

**Material.**—Three specimens, from locality HMF2: (1) external and internal moulds of two ventral valves, NU-B371, 372; (2) external mould of a ventral valve, NU-B373.

**Description.**—Shell medium size for genus, transverse outline; length about 12 mm, width 14 mm+ in the best preserved specimen (NU-B371). Ventral valve gently and evenly convex in lateral profile; sulcus with median fold occupying whole length of sulcus. External surface of ventral valve ornamented by numerous capillae, having a density of 6 per 1 mm near anterior margin.

**Remarks.**—This species resembles the shells, described as *Mesolobus sinuosa* (Schellwien, 1898) by Hayasaka (1925, p. 93, pl. 5, figs. 5, 6) and *Mesolobus* sp. by Tazawa (1979, p. 25, pl. 4, figs. 2a, b), from the lower Kanokura Formation of the southern Kitakami Mountains, in size of ventral valve and characters of sulcus. But the Moribu specimens are inadequate for detailed comparison.

Suborder Productidina Waagen, 1883  
Superfamily Productoidea Gray, 1840  
Family Productellidae Schuchert, 1929  
Subfamily Marginiferinae Stehli, 1954  
Tribe Paucispinerini Muir-Wood and Cooper, 1960  
Genus *Transennatia* Waterhouse, 1975

**Type species.**—*Productus graciosus* Waagen, 1884.

### *Transennatia graciosus* (Waagen, 1884)

Figure 6.1–6.7

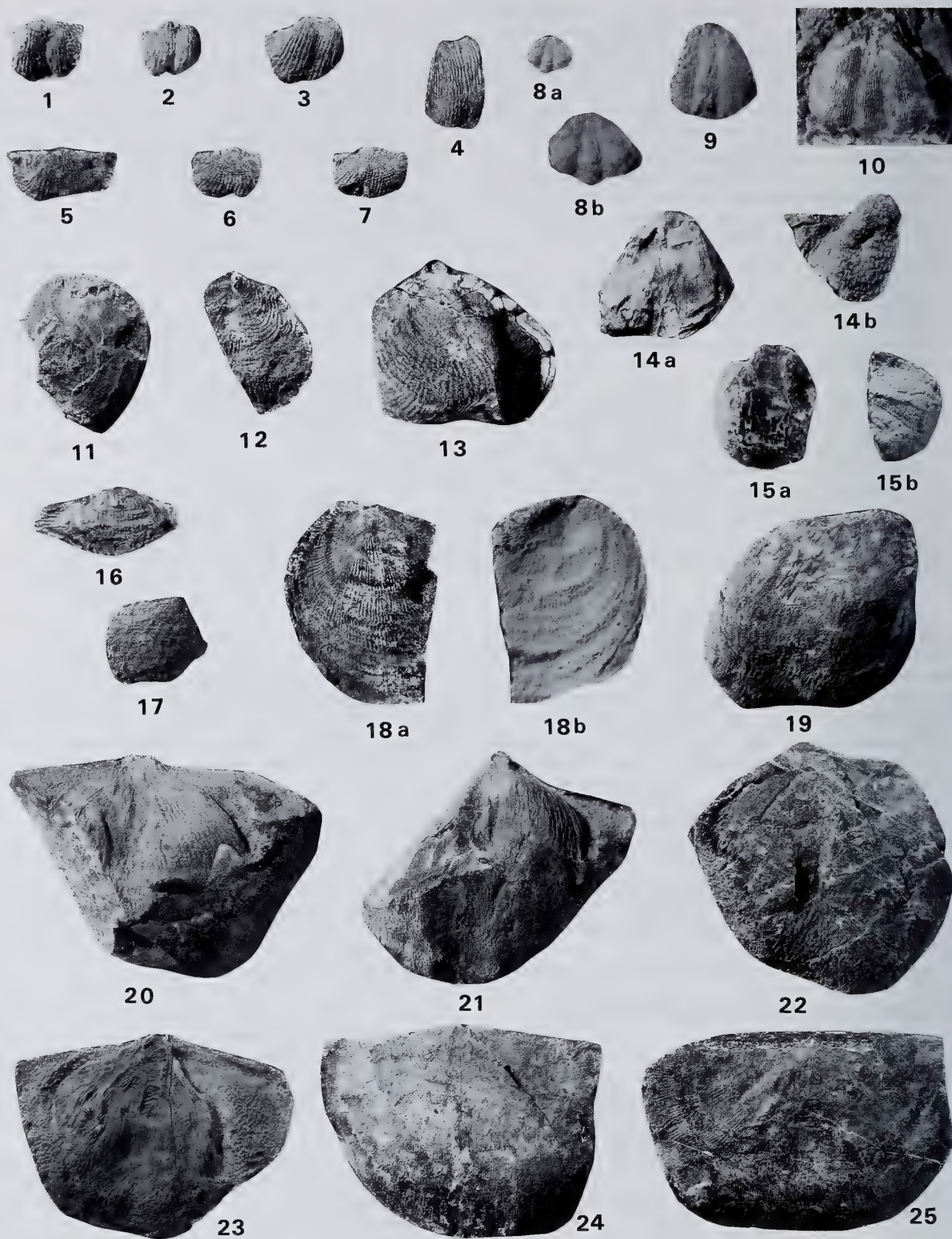
*Productus graciosus* Waagen, 1884, p. 691, pl. 72, figs. 3–7; Diener, 1897, p. 23, pl. 3, figs. 3–7; Mansuy, 1913, p. 115, pl. 13, figs. 1a, b; Colani, 1919, p. 10, pl. 1, figs. 2a–c; Chao, 1927, p. 44, pl. 4, figs. 6–10; Chi-Thuan, 1962, p. 491, pl. 2, figs. 5–7.  
*Productus (Dictyoclostus) graciosus* Waagen. Huang, 1933, p. 88, pl. 11, figs. 14a, b; Hayasaka, 1960, p. 49, pl. 1, fig. 8.  
*Marginifera graciosus* (Waagen). Reed, 1944, p. 98, pl. 19, figs. 6–7.  
*Dictyoclostus graciosus* (Waagen). Zhang and Ching, 1961, p. 411, pl. 4, figs. 12–18; Wang *et al.*, 1964, p. 291, pl. 45, figs. 14–19.  
*Gratosina graciosus* (Waagen). Grant, 1976, pl. 33, figs. 19–26; Licharew and Kotlyar, 1978, pl. 12, figs. 5, 6; pl. 20, figs. 1a, b; Minato *et al.*, 1979, pl. 61, figs. 11–13.  
*Asioproductus graciosus* (Waagen). Yang *et al.*, 1977, p. 350, pl. 140, figs. 5a–c; Feng and Jiang, 1978, p. 254, pl. 90, figs. 1–2; Tong, 1978, p. 228, pl. 80, figs. 7a, b; Lee *et al.*, 1980, p. 373, pl. 164, figs. 14a–c; pl. 166, figs. 5–6.  
*Asioproductus bellus* Chan (Zhan), 1979, p. 85, pl. 6, figs. 7–13; pl. 9, figs. 8–10; text-fig. 18.  
*Gratosina* sp. Minato *et al.*, 1979, pl. 61, fig. 14; Tazawa, 1991, p. 215.  
*Transennatia graciosus* (Waagen). Liu *et al.*, 1982, p. 185, pl. 132, figs. 9a–d; Wang *et al.*, 1982, p. 214, pl. 92, figs. 6–8; pl. 102, figs. 4–9; Ding and Qi, 1983, p. 280, pl. 95, figs. 14a, b.  
*Transennatia graciosus* (Waagen). Yang, 1984, p. 219, pl. 33, figs. 7a–c; Jin, 1985, pl. 4, figs. 33, 34, 45, 46; Tazawa and Matsumoto, 1998, p. 6, pl. 1, figs. 4–8; Tazawa, Takizawa and Kamada, 2000, p. 7, pl. 1, figs. 3–5; Tazawa, 2000, figs. 3.6, 3.7; Tazawa and Ibaraki, 2001, p. 7, pl. 1, figs. 1–3.

**Material.**—Ten specimens, from localities HMF2, 13: (1) external and internal moulds of two ventral valves, NU-B374, 375; (2) external casts of two ventral valves, NU-B376, 377; (3) external mould of a ventral valve, NU-B378; (4) internal moulds of two ventral valves, NU-B379, 380; (5) external moulds of three dorsal valves, NU-B381–383.

**Description.**—Shell small for genus, transversely subquadrate in outline, widest at hinge; length 9 mm, width 11 mm in the best preserved ventral valve specimen (NU-B374); length 11 mm+, width 21 mm in the largest dorsal valve specimen (NU-B382). Ventral valve strongly and unevenly convex in lateral profile, most convex at umbonal region, slightly geniculated at anterior margin of visceral disc, with long trail; umbo small, slightly incurved; ears small, distinct and pointed; sulcus narrow and deep; lateral slopes steep. Dorsal valve almost flat on visceral disc, slightly geniculated at anterior margin of visceral disc, followed by short trail; fold narrow and low. External surface of ventral valve reticulate on visceral disc, costate on trail; costae converging into sulcus anteriorly, having a density of 7–8 per 5 mm at midtrail; spines or spine bases not observed. External ornament of dorsal valve similar to that of opposite valve.

**Remarks.**—*Transennatia graciosus* (Waagen, 1884) was originally described by Waagen (1884) from the Wargal and Chhidru Formations of the Salt Range. The Moribu specimens are smaller than the Salt Range specimens, and most resemble the smaller shells of *T. graciosus*, from the Middle







Permian (Murgabian-Midian) of the southern Kitakami Mountains (Hayasaka, 1960, p. 49, pl. 1, fig. 8), South Primorye, eastern Russia (Licharew and Kotlyar, 1978, pl. 12, figs. 5, 6; pl. 20, figs. 1a, b) and Heilongjiang and Jilin, northeast China (Lee *et al.*, 1980, p. 373, pl. 164, figs. 14 a-c; pl. 166, figs. 5, 6).

*Transennatia insculpta* (Grant, 1976, p. 135, pl. 32, figs. 1-37; pl. 33, figs. 1-16) from the Rat Buri Limestone of Ko Muk, southern Thailand, is close to *T. gratiosa* in general appearance, but has wider shell and more prominent ears.

*Transennatia huananensis* (Zhan, 1979, p. 86, pl. 6, figs. 14-16) from the Longtan Formation of Guangdong, south China, is also a small *Transennatia*, but the Chinese species differs from *T. gratiosa* in having finer costae on the ventral valve.

**Distribution.**—Middle Permian (Murgabian-Midian) of Nepal (Kumaon Himalayas), Cambodia (Sisophon), Vietnam (Quang Tri), south China (Guangxi, Hubei and Shaanxi), northeast China (Jilin and Heilongjiang), eastern Russia (South Primorye) and Japan (Hida Gaien and South Kitakami Belts); Middle Permian (Murgabian) to Upper Permian (Dzhulfian) of Pakistan (Salt Range); Upper Permian (Dzhulfian) of south China (Sichuan, Guizhou, Guangdong, Hunan, Hubei, Jiangxi, Zhejiang and Anhui).

Subfamily Plicatiferinae Muir-Wood and Cooper, 1960

Tribe Yakovleviini Waterhouse, 1975

Genus *Yakovlevia* Fredericks, 1925

**Type species.**—*Yakovlevia kaluzinensis* Fredericks, 1925.

*Yakovlevia kaluzinensis* Fredericks, 1925

Figure 6.20-6.25

*Chonetes* (*Yakovlevia*) *kaluzinensis* Fredericks, 1925, p. 7, pl. 2, figs. 64-66.

*Yakovlevia kaluzinensis* Fredericks. Muir-Wood and Cooper, 1960, pl. 133, figs. 5, 6; Kotlyar, 1961, figs. 1-3; Licharew and Kotlyar, 1978, pl. 14, figs. 1, 2; Manankov, 1998, pl. 8, figs. 18, 19; Tazawa, 1999a, figs. 2.4-6; Tazawa, 1999b, p. 90, figs. 3.7-15; Tazawa, 2000, fig. 3.18.

*Yakovlevia* sp. Horikoshi *et al.*, 1987, figs. 3A, B; Tazawa, 1987, fig. 1.7.

**Material.**—Fourteen specimens, from localities HMF5, 12, 14, 25: (1) external mould of a dorsal valve and associated

internal mould of the conjoined valve, NU-B192; (2) external and internal moulds of a ventral valve, NU-B157; (3) internal moulds of seven ventral valves, NU-B158-160, 193-196; (4) external moulds of three dorsal valves, NU-B163, 164, 191; (5) internal moulds of two dorsal valves, NU-B161, 162.

**Description.**—Shell large for genus, transversely rectangular in outline, with greatest width at hinge; length about 37 mm, width about 44 mm in the smaller, but well preserved ventral valve specimen (NU-B157); length about 47 mm, width about 64 mm in the largest dorsal valve specimen (NU-B191).

Ventral valve gently convex on venter, strongly geniculated and followed by long trail; umbo small; ears large, prominent, but not clearly differentiated from visceral part; sulcus narrow and shallow, originating near umbo and extending to anterior margin. External ornament of ventral valve invisible except for a row of oblique spines just anterior to posterior margin. Dorsal valve almost flat on venter and strongly geniculated; fold narrow and low on anterior half of valve. External surface of dorsal valve ornamented by numerous fine costellae, with a density of 11-13 per 5 mm at midvalve.

Ventral valve interior with a pair of small, elongate subtrigonal adductor scars and two large diductor scars; diductor scars striated anteriorly and demarcated by a strong ridge posterolaterally. Internal structures of dorsal valve obscure in the present material.

**Remarks.**—The Moribu specimens are referred to *Yakovlevia kaluzinensis* Fredericks, 1925, originally described by Fredericks (1925) from the Chandalaz Formation of the Vladivostok area, South Primorye in size and shape of the shells, in particular, the transversely rectangular outline.

*Yakovlevia impressa* (Toula, 1875, p. 236, pl. 5, figs. 1a-c) from the Middle Permian of Spitsbergen differs from *Y. kaluzinensis* in having larger and more prominent ears.

**Distribution.**—Middle Permian (Kubergandian-Midian) of southeastern Mongolia (near Mt. Dzhirem-Ula), eastern Russia (South Primorye) and central Japan (Hida Gaien Belt).

Family Productidae Gray, 1840

Subfamily Dictyoclostinae Stehli, 1954

Genus *Reticulatia* Muir-Wood and Cooper, 1960

**Type species.**—*Productus huecoensis* King, 1931.

← **Figure 6.** 1-7. *Transennatia gratiosa* (Waagen), 1: Internal mould of a ventral valve, NU-B375, 2: Internal mould of a ventral valve, NU-B374, 3: External cast of a ventral valve, NU-B377, 4: External cast of a ventral valve, NU-B376, 5: External mould of a dorsal valve, NU-B382, 6: External mould of a dorsal valve, NU-B383, 7: External mould of a dorsal valve, NU-B381, 8a-10. *Capillomesolobus* sp., 8a, 8b: External latex cast of ventral valve, NU-B373, (8b x2), 9: External latex cast of a ventral valve, NU-B372, (x2), 10: Internal mould of a ventral valve, NU-B371, (x2), 11. *Orbiculoidea* cf. *jangarensis* Ustritsky, external mould of a ventral valve, NU-B370, 12, 13. *Reticulatia* sp., 12: External mould of a dorsal valve, NU-B477, 13: External mould of a dorsal valve, NU-B476, 14a-15b. *Juresania* cf. *juresanensis* (Tschernyschew), 14a, 14b: Internal mould and external latex cast of a ventral valve, NU-B384, 15a, 15b: Internal mould and lateral view of external latex cast of a ventral valve, NU-B385, 16. *Megousia* sp., external mould of a dorsal valve, NU-B404, 17. *Cancrinella* cf. *spinosa* Hayasaka and Minato, external cast of a ventral valve, NU-B397, 18a-19. *Linoproductus lineatus* (Waagen), 18a, 18b: External mould and external latex cast of a dorsal valve, NU-B396, 19: External cast of a ventral valve, NU-B395, 20-25. *Yakovlevia kaluzinensis* Fredericks, 20: Internal mould of a ventral valve, NU-B158, 21: Internal mould of a ventral valve, NU-B159, 22: Internal mould of a ventral valve, NU-B160, 23: Internal mould of a ventral valve, NU-B193, 24: Internal mould of a dorsal valve, NU-B161, 25: External mould of a dorsal valve, NU-B163. (Natural size unless otherwise indicated).



***Reticulatia* sp.**

Figure 6.12, 6.13

**Material.**—Two specimens, from locality HMF2, external moulds of two dorsal valves, NU-B476, 477.

**Description.**—Shell small for genus, slightly transverse subquadrate in outline; length about 29 mm, width about 34 mm in the larger specimen (NU-B476). Dorsal valve flat on disk, strongly geniculated and followed by short trail. External surface of dorsal valve ornamented by regular numerous rugae and costae on disc, costae only on trail; costae numbering 5 in 5 mm at anterior margin of disc. Internally, dorsal valve having strong cardinal process; other details not observed.

**Remarks.**—These specimens are safely assigned to the genus *Reticulatia* by its shape and external ornament of the dorsal valve. However, the specific identification is difficult because of the poor preservation.

Superfamily Echinoconchoidea Stehli, 1954

Family Echinoconchidae Stehli, 1954

Subfamily Juresaniinae Muir-Wood and Cooper, 1960

Tribe Juresaniini Muir-Wood and Cooper, 1960

Genus *Juresania* Fredericks, 1928

**Type species.**—*Productus juresanensis* Tschernyschew, 1902.

***Juresania* cf. *juresanensis* (Tschernyschew, 1902)**

Figure 6.14a–6.15b

**Compare.**—

*Productus juresanensis* Tschernyschew, 1902, p. 276, 620, pl. 29, figs. 1–2; pl. 47, figs. 1–2; pl. 53, figs. 4a, b; Fredericks, 1925, p. 27, pl. 4, figs. 118, 119.

*Buxtonia juresanensis* (Tschernyschew). Chao, 1927, p. 81, pl. 8, figs. 4–8; Czarniecki, 1969, p. 282, pl. 7, figs. 1–10; pl. 8, figs. 1–5; pl. 9, figs. 1–5; Sarytcheva and Sokolskaya, 1952, p. 102, pl. 17, fig. 117.

*Productus (Juresania) juresanensis* (Tschernyschew). Ozaki, 1931, p. 107, pl. 10, figs. 5a–c.

*Productus juresanensis typicus* Miloradovich, 1935, p. 79, 140, pl. 5, figs. 22–26; text-fig. 29.

*Juresania juresanensis* (Tschernyschew). Grabau, 1936, p. 140, pl. 13, figs. 5–6; Gobbett, 1963, p. 82, pl. 4, figs. 34–37; Nakamura, 1959, p. 203, pl. 2, figs. 1a–c; Yanagida, 1967, p. 52, pl. 15, figs. 1–7; text-fig. 4; Kalashnikov, 1980, p. 40, pl. 8, figs. 10a–v; Lazarev, 1982, p. 70, pl. 8, figs. 8–11; Liu *et al.*, 1982, p. 207, pl. 79, figs. 10a–c; Zhang *et al.*, 1983, p. 293, pl. 131, figs. 2a, b; Zeng, 1990, p. 217, pl. 4, figs. 9a–c; Fan and He, 1999, p. 119, pl. 10, figs. 9–10.

**Material.**—Two specimens, from locality HMF5, external and internal moulds of two ventral valves, NU-B384, 385.

**Description.**—Shell medium size for genus, longer than wide; length about 26 mm, width about 22 mm in the smaller but better preserved specimen (NU-B385). Ventral valve strongly convex in both lateral and anterior profiles, with small, convex ears, shallow sulcus and very steep lateral slopes. External ornament of ventral valve consisting of

regular concentric bands and numerous spine bases of two sizes on them; smaller spine bases sometimes occur between larger ones on anterior half of valve.

**Remarks.**—In external character the Moribu specimens resemble well the ventral valves of *Juresania juresanensis* (Tschernyschew, 1902), from the Lower Permian Indiga Horizon of Timan (Tschernyschew, 1902, pl. 29, figs. 1a–c) and from the Maping Limestone of Yunnan Province, south China (Grabau, 1936, pl. 13, figs. 5–6). But the poor preservation of this material makes accurate comparison difficult. *J. juresanensis* has been described from the Middle Carboniferous (Moscovian) to the Middle Permian (Midian) of Spitsbergen, northern Russia (Novaya Zemlya, Urals, Timan, Kanin Peninsula and Moscow Basin), northern Thailand, south China (Yunnan), northwest China (Xinjiang and Gansu), north China (Inner Mongolia, Shanxi and Shandong), eastern Russia (South Primorye), and northeast Japan (South Kitakami Belt).

Tribe Waagenoconchini Muir-Wood and Cooper, 1960

Genus *Waagenoconcha* Chao, 1927

**Type species.**—*Productus humboldtii* d'Orbigny, 1842.

***Waagenoconcha permocarbonica*** Ustritsky, in Ustritsky and Tschernjak, 1963

Figure 7.20–7.23

*Waagenoconcha permocarbonica* Ustritsky, in Ustritsky and Tschernjak, 1963, p. 79, pl. 7, fig. 6; pl. 8, figs. 1–3; Lee *et al.*, 1980, p. 364, pl. 168, figs. 1, 6; pl. 169, figs. 3, 4; Duan and Li, 1985, p. 107, pl. 37, figs. 3–5; Shi and Waterhouse, 1996, p. 77, pl. 9, figs. 4–15; pl. 10, figs. 1–4; Tazawa, 2000, figs. 3.16, 3.17.

**Material.**—Eight specimens, from locality HMF12: (1) external and internal moulds of a conjoined valve, NU-B386; (2) internal moulds of a conjoined valve, NU-B387; (3) external moulds of two ventral valves, NU-B388, 389; (4) external and internal moulds of two dorsal valves, NU-B390, 391; (5) external moulds of two dorsal valves, NU-B392, 393.

**Description.**—Shell large for genus, transverse, subrectangular in outline, with greatest width slightly anterior to midvalve; length 49 mm, width 51 mm in a ventral valve specimen (NU-B388). Ventral valve strongly convex in both lateral and anterior profiles, with steep lateral slopes; sulcus moderately developed, originating at about 8–10 mm from umbo, deepest at midvalve, and shallowing and widening anteriorly. Dorsal valve with low fold, flat on visceral disc, moderately geniculated, and followed by short trail. External surface of ventral valve ornamented by irregular concentric rugae and numerous, quincuncially arranged spine bases; spine bases becoming fine at anterolateral parts; numbering 5–6 in 5 mm at midvalve, 15–17 in 5 mm near anterior margin. External ornament of dorsal valve similar to that of opposite valve. Internal structures of both valves obscure.

**Remarks.**—These specimens are referred to *Waagenoconcha permocarbonica* Ustritsky, 1963, originally described by Ustritsky (in Ustritsky and Tschernjak, 1963) from the Bashkirian to the Sakmarian of Taimyr, on account of size,



shape and external ornament of both valves.

*Waagenoconcha* sp. B, described and figured by Liu and Waterhouse (1985, p. 15, pl. 2, figs. 3, 4) from the Middle Permian Zhesi (Jisu) Formation of Xiujimqinqi, Inner Mongolia, differs from the present species in its less transverse outline.

*Waagenoconcha waageni* (Rothpletz, 1892) from the Middle Permian of Timor is close in general outline, but it has more numerous and stronger concentric bands and coarser spine bases on the ventral valve (see Archbold and Bird, 1989, figs. 3C, D).

**Distribution.**—Middle Carboniferous (Bashkirian) to Lower Permian (Sakmarian) of northern Russia (Taimyr); Lower Permian (Sakmarian) of western Canada (Yukon Territory); Middle Permian (Kubergandian-Murgabian) of north China (Inner Mongolia), northeast China (Jilin and Heilongjiang) and central Japan (Hida Gaien Belt).

***Waagenoconcha* cf. *imperfecta* Prendergast, 1935**

Figure 7.24a, 7.24b

**Compare.**—

*Waagenoconcha imperfecta* Prendergast, 1935, p. 15, pl. 4, figs. 1–3; Prendergast, 1943, p. 25, pl. 3, figs. 7–9; Coleman, 1957, p. 82, pl. 10, figs. 8–14; pl. 11, figs. 1–6; Tazawa, 1974b, p. 127, pl. 1, figs. 4–6; pl. 2, figs. 2–7; pl. 3, figs. 1–3; pl. 4, figs. 1–4, 7. *Waagenoconcha* (*Wimanoconcha*) *imperfecta* Prendergast. Archbold, 1993, p. 20, figs. 11A–H, 12A–K, 13A–G.

**Material.**—One specimen, from locality HMF2, external and internal moulds of a dorsal valve, NU-B394.

**Remarks.**—The single dorsal valve specimen from Moribu is small in size (length 27 mm, width 29 mm), almost flat on venter, with a low and wide fold on the anterior half of the valve, weakly geniculated, and ornamented by numerous, fine, quincuncially arranged spine bases, having a density of 8 per 5 mm at the midvalve. This specimen may be a young shell of *Waagenoconcha imperfecta* Prendergast, 1935, which has been described from the Upper Permian (Dzhulfian) Hardman Formation of the Canning Basin, western Australia (Prendergast, 1935, 1943; Coleman, 1957; Archbold, 1993) and the Middle Permian (Murgabian) lower Kanokura Formation of the southern Kitakami Mountains, northeast Japan (Tazawa, 1974b). *W. imperfecta* is distinguished from any other waagenoconchids by its very fine and closely arranged spine bases on both the ventral and dorsal valves.

Superfamily Linoproductoidea Stehli, 1954

Family Linoproductidae Stehli, 1954

Subfamily Linoproductinae Stehli, 1954

Genus *Linoproductus* Chao, 1927

**Type species.**—*Productus cora* d'Orbigny, 1842.

***Linoproductus lineatus* (Waagen, 1884)**

Figure 6.18a–6.19

*Productus lineatus* Waagen, 1884, p. 673, pl. 66, figs. 1–2; pl. 67, fig. 3; text-figs. 21a–d; Diener, 1903, p. 138, pl. 7, figs. 1a–c;

Tschernyschew, 1914, p. 30, 63, pl. 10, figs. 1a–c.

*Productus* (*Linoproductus*) *lineatus* (Waagen). Grabau, 1931, p. 293, pl. 29, figs. 25–27.

*Linoproductus lineatus* (Waagen). Chao, 1927, p. 129, pl. 15, figs. 25–27; Ivanov, 1935, p. 105, pl. 5, fig. 6; pl. 6, figs. 1–4; Minato, 1943, p. 54, pl. 2, figs. 2–5; Sarytcheva and Sokolskaya, 1952, p. 115, pl. 21, fig. 149; Volgin, 1960, p. 70, pl. 7, figs. 2a–v; Lee and Gu, 1976, p. 259, pl. 162, fig. 10; Feng and Jiang, 1978, p. 260, pl. 92, figs. 4a, b; Licharew and Kotlyar, 1978, pl. 13, fig. 1; Tong, 1978, p. 231, pl. 81, figs. 7a, b; Lee *et al.*, 1980, p. 376, pl. 152, fig. 13; Yang, 1984, p. 222, pl. 34, figs. 14a, b; Sremac, 1986, p. 28, pl. 9, figs. 9a–c; Wang and Yang, 1998, p. 100, pl. 16, figs. 1, 3–6.

*Linoproductus lineatus lineatus* (Waagen). Ramovs, 1958, p. 515, 592, pl. 6, figs. 1a–c; pl. 7, figs. 1a–c; pl. 8, figs. 1a, b.

*Linoproductus* cf. *lineatus* (Waagen). Yanagida, 1963, p. 74, pl. 10, figs. 8–14.

*Linoproductus lineata* (Waagen). Ding and Qi, 1983, p. 291, pl. 99, figs. 3a–c.

**Material.**—Two specimens, from localities HMF2, 8: (1) external cast of a ventral valve, NU-B395; (2) external mould of a dorsal valve, NU-B396.

**Remarks.**—The specimens from Moribu are referred to *Linoproductus lineatus* (Waagen, 1884), originally described by Waagen (1884) from the Amb, Wargal and Chhidru Formations of the Salt Range, because of similarities in size, shape and external ornament. The ventral valve specimen (NU-B395) is elongate in outline (length 44 mm, width 40 mm), and has small ears and a shallow sulcus. The dorsal valve specimen (NU-B396) is also longer than wide, with a rather short hinge line, and ornamented by numerous costellae (8–10 per 5 mm at the midvalve) and irregular, strong concentric rugae.

The type species, *Linoproductus cora* (d'Orbigny, 1842), from the Lower Permian of Bolivia, differs from *L. lineatus* in its larger, transverse shell and in having much larger ears and lacking a ventral sulcus (see Muir-Wood and Cooper, 1960, pl. 111, figs. 3–6).

**Distribution.**—Middle Carboniferous (Moscovian) of northeast China (Jilin); Upper Carboniferous (Kasimovian-Gzhelian) of Russia (Moscow Basin and southern Fergana); Lower Permian of northwest China (Xinjiang); Lower Permian (Asselian) to Upper Permian (Dzhulfian) of Croatia, Pakistan (Salt Range), India (Spiti, Punjab Himalayas), Fergana, south China (Guizhou, Sichuan and Hubei), northwest China (Gansu), north China (Inner Mongolia), northeast China (Jilin), eastern Russia (South Primorye) and Japan (Mizukoshi in Kyushu Island and Moribu in the Hida Mountains).

Subfamily Anidanthinae Waterhouse, 1968

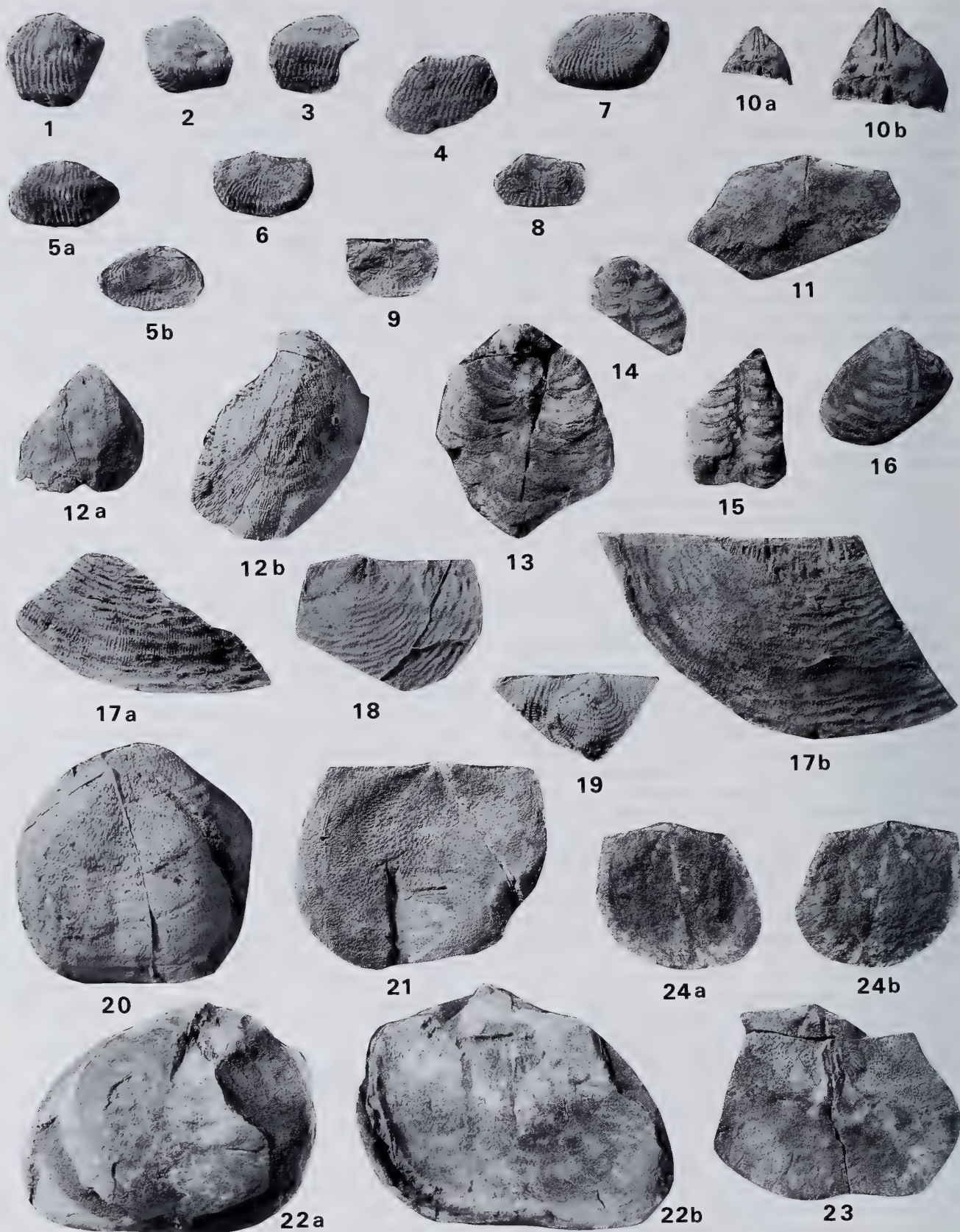
Genus *Megousia* Muir-Wood and Cooper, 1960

**Type species.**—*Megousia auriculata* Muir-Wood and Cooper, 1960.

***Megousia* sp.**

Figure 6.16







*Megousia* sp. Tazawa, 2000, fig. 3.3.

**Material.**—One specimen, from locality HMF2, external mould of a dorsal valve, NU-B404.

**Remarks.**—This specimen is safely assigned to the genus *Megousia* on the basis of its small size, transversely elliptical outline (length 11 mm, width 26 mm), and in having greatly developed ears with radial ornament. The Moribu species superficially resembles *Megousia solita* Waterhouse (1968, p. 1172, pl. 154, figs. 1–6, 8–10), from the Middle Permian Ulladulla Formation of New South Wales, eastern Australia, but the material is too poor for comparison.

*Megousia koizumii* Nakamura (1972, p. 438, pl. 2, figs. 1, 4, 5), from the Middle Permian Kashiwadaira Formation of the Takakurayama area, Abukuma Mountains, northeast Japan, is clearly distinguished from the present species by its larger, recurved and hung down ears.

Subfamily Grandaurispininae Lazarev, 1986  
Genus *Cancrinella* Fredericks, 1928

**Type species.**—*Productus cancrini* de Verneuil, 1845.

*Cancrinella* cf. *spinosa* Hayasaka and Minato, 1956

Figure 6.17

**Comapare.**—

*Productus villiersi kozlowskianus* Fredericks. Hayasaka, 1925, p. 96, pl. 5, figs. 10, 11.

*Cancrinella cancriniformis spinosa* Hayasaka and Minato, 1956, p. 144, pl. 23, figs. 4a, b.

*Cancrinella spinosa* Hayasaka and Minato. Tazawa, 1976, pl. 2, fig. 5; Minato *et al.*, 1979, pl. 62, figs. 5–8, 11.

**Material.**—One specimen, from locality HMF2, external cast of a ventral valve, NU-B397.

**Remarks.**—The fragmentarily preserved specimen is assigned to the genus *Cancrinella* on the basis of its small sized ventral valve (length 18 mm +, width 16 mm +), lacking sulcus, and ornamented by fine concentric rugae and numerous, quincuncially arranged spine bases on the venter.

This specimen can be safely assigned to the *Cancrinella cancriniformis* group of Grigoreva *et al.* (1977) by having distinct rugae on the ventral valve. Within the group, the Moribu species is closely allied to *Cancrinella spinosa*

Hayasaka and Minato, 1956, described from the Middle Permian (Murgabian) lower Kanokura Formation of the southern Kitakami Mountains (Hayasaka, 1925; Hayasaka and Minato, 1956; Tazawa, 1976; Minato *et al.*, 1979) in size, shape and external ornament of the ventral valve.

Family Monticuliferidae Muir-Wood and Cooper, 1960  
Subfamily Compressoproductinae Jin and Hu, 1978  
Genus *Fallaxoproductus* Lee, Gu and Li, 1982

**Type species.**—*Fallaxoproductus sutungensis* Lee, Gu and Li, 1982.

*Fallaxoproductus moribuensis* sp. nov.

Figure 7.12a, 7.12b

**Material.**—Two specimens, from locality HMF12: (1) external and internal moulds of a ventral valve (holotype), NU-B398; (2) external mould of a ventral valve, NU-B399.

**Diagnosis.**—Shell medium size for genus, slightly elongate trigonal, with very fine costellae on ventral valve, having a density of 12–14 in 5 mm near anterior margin.

**Description.**—Shell small to medium for genus, slightly elongate trigonal in outline, with short hinge, greatest width near anterior margin; length about 39 mm, width about 32 mm in the holotype (NU-B398). Ventral valve strongly convex on umbonal slope and slightly convex to nearly flat on anterior half of valve; beak prominent, strongly incurved, but not overhanging hinge line; without ears and sulcus. External surface of ventral valve ornamented by regular, numerous, fine costellae, numbering 12–14 in 5 mm near anterior margin; spines clustering along lateral margins; rugae completely absent. Internal structures of ventral valve obscure in the present material.

**Remarks.**—*Fallaxoproductus moribuensis* sp. nov. can be differentiated from the type and two other described species, *F. dedorus* Lee, Gu and Li, 1982 and *F. plenus* Lee, Gu and Li, 1982, both from the Lower Permian of the Xiujiminqi area, Inner Mongolia, by its fine costellae on the ventral valve.

The type species, *Fallaxoproductus sutungensis* Lee, Gu and Li, 1982, is much closer to *F. moribuensis* in size and outline of shell, but it differs from the latter in having fewer and more strong costellae on the ventral valve.

← **Figure 7.** 1–9. *Urushtenoidea crenulata* (Ting), 1: Internal mould of a ventral valve, NU-B407, 2: Internal mould of a ventral valve, NU-B411, 3: Internal mould of a ventral valve, NU-B409, 4: Anterior view of internal mould of a ventral valve, NU-B405, 5a, 5b: Ventral and dorsal views of internal mould of a conjoined valve, NU-B406, 6: External mould of a dorsal valve, NU-B416, 7: External mould of a dorsal valve, NU-B415, 8: Internal mould of a dorsal valve, NU-B418, 9: Internal mould of a dorsal valve, NU-B417, 10a, 10b. *Enteleles* sp., internal mould of a ventral valve, NU-B430, (10b x2), 11. *Derbyia* sp., internal mould of a ventral valve, NU-B429, 12a, 12b. *Fallaxoproductus moribuensis* sp. nov., internal mould and external latex cast of a ventral valve, NU-B398 (holotype), 13–16. *Leptodus nobilis* (Waagen), 13: Internal mould of a ventral valve, NU-B424, 14: Internal mould of a ventral valve, NU-B427, 15: Internal mould of a ventral valve, NU-B421, 16: Internal mould of a ventral valve, NU-B426, 17a–19. *Permudaria asiatica* Nakamura, Kato and Choi, 17a, 17b: External latex cast and internal mould of a ventral valve, NU-B400, 18: External latex cast of a ventral valve, NU-B402, 19: External latex cast of a ventral valve, NU-B403, 20–23. *Waagenoconcha permocarbonica* Ustritsky, 20: External latex cast of a ventral valve, NU-B388, 21: External mould of a dorsal valve, NU-B392, 22a, 22b: Ventral and dorsal views of internal mould of a conjoined valve, NU-B387, 23: Internal mould of a dorsal valve, NU-B390, 24a, 24b. *Waagenoconcha* cf. *imperfecta* Prendergast, internal and external moulds of a dorsal valve, NU-B394. (Natural size unless otherwise indicated).



Subfamily Schrenkiellinae Lazarev, 1986  
Genus *Permundaria* Nakamura, Kato and Choi, 1970

Type species.—*Permundaria asiatica* Nakamura, Kato and Choi, 1970.

*Permundaria asiatica* Nakamura, Kato and Choi, 1970

Figure 7.17a–7.19

*Striatifera?* sp. Hayasaka and Minato, 1956, p. 144, pl. 23, figs. 6, 7.  
*Permundaria asiatica* Nakamura, Kato and Choi, 1970, p. 296, pl. 2, figs. 1, 2; Tazawa, 1974a, p. 315, pl. 43, figs. 3–4; Minato *et al.*, 1979, pl. 62, figs. 12, 13; Tazawa, 2000, fig. 3.4.

**Material.**—Four specimens, from locality HMF12, external and internal moulds of four ventral valves, NU-B400–403.

**Remarks.**—Among the specimens from Moribu, the largest ventral valve specimen (NU-B400) may have originally been about 45 mm long, and about 70 mm wide, although both the anterior portion and left half of the valve have been broken off. The valve is slightly convex in the lateral and anterior profiles, and is ornamented by irregularly developed and somewhat flexuous concentric rugae and numerous costellae, numbering 11–12 in 5 mm near the anterior margin. Another specimen (NU-B403) is also an imperfect ventral valve, but the posterior part is well preserved. The ventral valve has a straight hinge, large and flattened ears, and a small, pointed and slightly elevated umbo.

These specimens can be identified with *Permundaria asiatica* Nakamura, Kato and Choi, 1970 by having a small and pointed umbo, irregular and slightly flexuous rugae, and relatively coarse costellae on the ventral valves. *P. asiatica* was originally described by Nakamura *et al.* (1970, p. 296) based on two specimens, the holotype from the lower Kanokura Formation of the southern Kitakami Mountains, northeast Japan, and the paratype from the Sisophon Limestone (*Yabeina* Zone) of Sisophon, Cambodia. The present species is easily distinguished from the following three *Permundaria* species in having coarser costellae on both valves: *P. sisophonensis* Nakamura, Kato and Choi (1970, p. 297, pl. 2, figs. 3a, b) from the Sisophon Limestone of Cambodia, *P. tenuistriata* Tazawa (1974a, p. 317, pl. 43, figs. 1, 2) from the lower Kanokura Formation of the southern Kitakami Mountains, and *P. liaoningensis* Lee and Gu (in Lee *et al.*, 1980, p. 385, pl. 172, figs. 5–8) from the Lower Permian of Liaoning and Heilongjiang, northeast China.

*Permundaria shizipuensis* Jin, Liao and Fang (1974, p. 310, pl. 162, fig. 18) from the Maokou Formation of Guizhou, south China, differs from *P. asiatica* in having a massive and rounded umbo on the ventral valve.

**Distribution.**—Middle Permian (Murgabian-Midian) of Cambodia and Japan (South Kitakami and Hida Gaien Belts).

Suborder Strophalosioidina Schuchert, 1913  
Superfamily Aulostegoidea Muir-Wood and Cooper, 1960  
Family Aulostegidae Muir-Wood and Cooper, 1960  
Subfamily Chonosteginae Muir-Wood and Cooper, 1960  
Genus *Urushtenoidea* Jin and Hu, 1978

Type species.—*Urushtenia chaoi* Jin, 1963.

*Urushtenoidea crenulata* (Ting, in Yang *et al.*, 1962)

Figure 7.1–7.9

*Eomarginifera crenulata* Ting, in Yang *et al.*, 1962, p. 85, pl. 37, figs. 6 right–8.

*Urushtenia costata* Ting, in Yang *et al.*, 1962, p. 87, pl. 25, figs. 5–7; pl. 37, fig. 6 left.

*Urushtenia chenanensis* Chan, in Chan (Zhan) and Lee, 1962, p. 478, 488, pl. 3, figs. 4–6; Tong, 1978, p. 218, pl. 78, figs. 16a–c.

*Urushtenia crenulata* (Ting). Jin, 1963, p. 20, pl. 1, figs. 17–24; pl. 2, figs. 9, 10, 18–20; text-fig. 5; Yang *et al.*, 1977, p. 335, pl. 136, figs. 11a–c; Feng and Jiang, 1978, p. 246, pl. 89, figs. 11a, b; Tong, 1978, p. 218, pl. 78, figs. 17a–c; Yang and Gao, 1996, pl. 34, figs. 7–8.

*Urushtenoidea chenanensis* (Chan). Jin and Hu, 1978, p. 117, pl. 2, fig. 9; Hu, 1983, pl. 3, figs. 4–5.

*Urushtenoidea maceus* (Ching). Nakamura, 1979, p. 227, pl. 1, figs. 1–4; pl. 2, figs. 1–3; Minato *et al.*, 1979, pl. 65, figs. 8–11.

*Urushtenoidea crenulata* (Ting). Nakamura, 1979, p. 228, pl. 1, figs. 5–9; pl. 3, figs. 1–2; Tazawa, 2000, figs. 3.10, 3.11.

*Uncisteges crenulata* (Ting). Liu *et al.*, 1982, p. 178, pl. 129, figs. 1a–d; Jin, 1985, pl. 6, fig. 41; Zhu, 1990, p. 74, pl. 14, figs. 4–14; pl. 17, figs. 12, 12a.

**Material.**—Fifteen specimens, from locality HMF2; (1) external mould of a ventral valve and associated internal mould of conjoined valve, NU-B405; (2) internal mould of a conjoined valve, NU-B406; (3) internal moulds of six ventral valves, NU-B407–412; (4) external and internal moulds of a dorsal valve, NU-B413; (5) external moulds of three dorsal valves, NU-B414–416; (6) internal moulds of three dorsal valves, NU-B417–419.

**Description.**—Shell medium size for genus, transversely subquadrate in outline; hinge straight, a little less than greatest width; the latter occurring at about midvalve; length 12 mm, width 19 mm in a smaller ventral valve specimen (NU-B406); length 12 mm, width 20 mm in a larger dorsal valve specimen (NU-B415).

Ventral valve strongly geniculated at right angle and followed by long trail; umbo small; lateral slopes steep; ears small; sulcus low and wide, originating at midvisceral disc. External ornament of ventral valve consisting of few weak concentric rugae and costae on visceral disc, numerous costae on trail; costae regular, straight and strong on trail, with a density of 6 per 5 mm at middle of trail; anterior half of ventral trail having some concentric rugae and row of spines on costae. Dorsal valve almost flat on visceral disc, strongly geniculated, and followed by short trail; fold low and wide. External ornament of brachial valve similar to that of opposite valve, but more distinct and regular reticulate ornament on visceral disc.

Interior of dorsal valve with a median septum, extending to midvalve, a pair of elongate muscle scars on both sides of median septum. Other internal structures not observed in the present specimens.

**Remarks.**—These specimens are identical with *Urushtenoidea crenulata* (Ting, in Yang *et al.*, 1962) in size, shape



and external ornament of shell, especially the density of costae on the ventral trail. *Urushtenoidea chenensis* (Chan, in Chan and Lee, 1962) is a synonym of the present species.

*Urushtenoidea maceus* (Jin, 1963), originally described and figured as *Urushtenia maceus* from the Middle Permian of Hubei, Anhui, Zhejiang and Jiangsu, south China (Jin, 1963, p. 19, pl. 2, figs. 1–6) somewhat resembles *U. crenulata* in size and outline, but the former differs from the latter in having much finer costae on the ventral valve.

**Distribution.**—Middle Permian (Murgabian-Midian) of Cambodia (Sisophon), south China (Guizhou, Sichuan, Hunan, Guangdong, Jiangxi, Fujian, Jiangsu, Hubei and Shaanxi), northwest China (Qinghai and Gansu), and Japan (South Kitakami and Hida Gaien Belts).

Superfamily Lyttonioidea Waagen, 1883

Family Lyttoniidae Waagen, 1883

Subfamily Lyttoniinae Waagen, 1883

Genus *Leptodus* Kayser, 1883

**Type species.**—*Leptodus richthofeni* Kayser, 1883.

*Leptodus nobilis* (Waagen, 1883)

Figure 7.13–7.16

*Lyttonia nobilis* Waagen, 1883, p. 398, pl. 29, figs. 1–3; pl. 30, figs. 1, 2, 5, 6, 8, 10, 11; Diener, 1897, p. 37, pl. 1, figs. 5–7; Noetling, 1904, p. 112, text-figs. 4–7; Noetling, 1905, p. 140, pl. 17, figs. 1, 2; pl. 18, figs. 1–11, text-fig. 2; Mansuy, 1913, p. 123, pl. 13, fig. 10; Mansuy, 1914, p. 32, pl. 6, figs. 7a–d; pl. 7, figs. 1a–e; Diener, 1915, p. 99, pl. 10, fig. 15; Albrecht, 1924, p. 289, figs. 1a, b; Grabau, 1931, p. 285, pl. 28, figs. 3–6; Huang, 1932, p. 89, pl. 7, figs. 9, 10; pl. 8, figs. 8, 9; pl. 9, figs. 1–8, text-figs. 8–11; Simic, 1933, p. 49, pl. 4, fig. 1.

*Lyttonia tenuis* Waagen, 1883, p. 401, pl. 30, figs. 3, 4, 7, 9.

*Lyttonia* sp. Yabe, 1900, p. 2, text-figs. 1, 2.

*Lyttonia* cf. *tenuis* Waagen. Mansuy, 1912, p. 19, pl. 4, fig. 4; pl. 5, figs. 1a–e; Huang, 1936, p. 493, pl. 1, fig. 6.

*Oldhamina* (*Lyttonia*) *richthofeni* var. *nobilis* Waagen. Fredericks, 1916, p. 76, pl. 4, fig. 2, text-fig. 22.

*Lyttonia richthofeni* (Kayser). Hayasaka, 1917, p. 43, pl. 18, figs. 1–8; Hayasaka, 1922a, p. 62, pl. 11, figs. 1–6; Hayasaka, 1922b, p. 103, pl. 4, figs. 12, 13; Fredericks, 1925, p. 14, pl. 3, figs. 105–107; Licharew, 1932, p. 56, 86, pl. 1, figs. 1–16; pl. 2, figs. 1, 2, 5, 7, 10, 12; pl. 3, figs. 2–7; pl. 4, figs. 1–17; pl. 5, figs. 1–4, 6; Mashiko, 1934, p. 182, text-fig.

*Lyttonia* (*Leptodus*) *richthofeni* Kayser. Hamlet, 1928, p. 31, pl. 6, figs. 1–4.

*Lyttonia richthofeni* forma *nobilis* Waagen. Licharew, 1932, p. 69, 96, pl. 2, figs. 13, 14; pl. 5, figs. 1–4, 6; text-fig. 3.

*Lyttonia* cf. *richthofeni* (Kayser). Huang, 1932, p. 87, pl. 8, figs. 4a, b.

*Leptodus nobilis* (Waagen). Wanner and Sieverts, 1935, p. 249, pl. 9, figs. 27, 28; text-figs. 16–18; Termier and Termier, 1960, p. 241, text-pl. 3, figs. 1–10; Chi-Thuan, 1961, p. 274, pl. 1, figs. 1a, b; Schr ter, 1963, p. 107, pl. 3, figs. 5–8; Sarytcheva, 1964, p. 65, pl. 7, figs. 5–8; text-fig. 1; Ruzhentsev and Sarytcheva, 1965, pl. 39, figs. 6–8; Cooper and Grant, 1974, pl. 191, figs. 8, 9; Grant, 1976, pl. 43, figs. 18, 19; Lee and Gu, 1976, p. 267,

pl. 162, figs. 1, 2; Tazawa, 1976, pl. 2, fig. 8; Yang *et al.*, 1977, p. 371, pl. 147, fig. 5; Feng and Jiang, 1978, p. 269, pl. 100, fig. 2; Licharew and Kotlyar, 1978, pl. 14, figs. 13–15; Jin *et al.*, 1979, p. 82, pl. 23, fig. 15; Minato *et al.*, 1979, pl. 66, figs. 1, 4, 5; Zhan, 1979, p. 93, pl. 9, fig. 12; Lee *et al.*, 1980, p. 389, pl. 172, figs. 15, 16; Wang *et al.*, 1982, p. 229, pl. 95, fig. 20; Zhan and Wu, 1982, pl. 4, fig. 4; Ding and Qi, 1983, p. 297, pl. 102, figs. 7, 8; Yang, 1984, p. 226, pl. 35, fig. 12; Gu and Zhu, 1985, pl. 1, figs. 31, 33, 34; Liao and Meng, 1986, p. 81, pl. 2, figs. 24, 25; Sremac, 1986, p. 30, pl. 10, figs. 1–2; Tazawa, 1987, fig. 1.11; Kotlyar, in Kotlyar and Zakharov, 1989, pl. 20, fig. 6; pl. 23, fig. 12; Liang, 1990, p. 225, pl. 40, figs. 1, 5; Tazawa and Matsumoto, 1998, p. 7, pl. 2, figs. 7–12; Tazawa *et al.*, 1998, p. 241, figs. 2.1, 2.2; Kato *et al.*, 1999, p. 47, figs. 4a, b; Tazawa, 2000, figs. 3.14, 3.15, 7.1a, 7.1b; Tazawa and Ibaraki, 2001, p. 11, pl. 1, figs. 7–10.

*Lyttonia* cf. *nobilis* Waagen. Huang, 1936, p. 493, pl. 1, fig. 5.

*Leptodus* cf. *nobilis* (Waagen). Thomas, 1957, p. 177, pl. 20, figs. 1–6.

*Leptodus richthofeni* Kayser. Shimizu, 1961, pl. 18, figs. 14, 15; Schr ter, 1963, p. 106, pl. 3, fig. 4; Sarytcheva, 1964, p. 65, pl. 7, figs. 2–4; Yang *et al.*, 1977, p. 372, pl. 147, fig. 10; Yang, 1984, p. 226, pl. 35, fig. 11; Duan and Li, 1985, p. 119, pl. 35, figs. 17–19.

*Leptodus ivanovi* Frederiks. Minato *et al.*, 1979, pl. 66, fig. 3.

*Leptodus* sp. Minato *et al.*, 1979, pl. 66, fig. 2.

*Leptodus tenuis* (Waagen). Yang, 1984, p. 226, pl. 35, fig. 13; Duan and Li, 1985, p. 119, pl. 35, figs. 14–16; Liang, 1990, p. 226, pl. 40, fig. 9; Zhu, 1990, p. 79, pl. 18, figs. 19–21.

*Leptodus* sp. Tazawa, 1987, fig. 1.10.

*Gubleria* sp. Zhu, 1990, p. 80, pl. 16, fig. 24.

**Material.**—Nine specimens, from locality HMF2: (1) external and internal moulds of three ventral valves, NU-B420–422; (2) external mould of a ventral valve, NU-B423; (3) internal moulds of five ventral valves, NU-B424–428.

**Description.**—Shell small to medium size for genus, elongate subtrigonal in outline, with greatest width near anterior margin; length 40 mm, width 32 mm in the largest specimen (NU-B424). Ventral valve almost flat, slightly convex in lateral and anterior profiles. Ventral valve interior with regularly and symmetrically arranged lateral septa on both sides of median septum; lateral septa broad and solid (solidiseptate), straight to slightly arched toward front, numbering 12 pairs in the largest specimen; interseptal spaces 2.0–2.5 mm in width; median septum highly developed.

**Remarks.**—These specimens are relatively small in size, and seem to be immature shells of *Leptodus nobilis* (Waagen, 1883), originally described by Waagen (1883, p. 398) from the Wargal and Chhidru Formations of the Salt Range. The Moribu specimens externally most resemble the shells, described as *Lyttonia richthofeni* (Kayser) by Hayasaka (1917, p. 43, pl. 18, figs. 1–6; Hayasaka, 1922a, p. 62, pl. 11, figs. 2, 3) from the lower Kanokura Formation of the southern Kitakami Mountains.

The type species, *Leptodus richthofeni* Kayser, 1883 from the Permian of Loping, Jiangxi Province, south China (Kayser, 1883, p. 161, pl. 21, figs. 9–11; Cooper and Grant, 1974, p. 411, pl. 191, figs. 11–15) differs from *L. nobilis* in having a more strongly convex ventral valve, with sharp lat-

eral septa and much broader interseptal spaces.

*Distribution*.—Middle Permian (Kubergandian) to Upper Permian (Dorashamian) of Hungary, Croatia, Serbia, western Russia (Caucasus Mountains), Pakistan (Salt Range and Khiser Range), India (Kashmir), Nepal (Kumaon Himalayas), Cambodia, Laos, Timor, northern Australia (Port Keats), northwest China (Tibet and Qinghai), south China (Yunnan, Guangxi, Guizhou, Sichuan, Hubei, Hunan, Guangdong, Jiangxi, Fujian and Zhejiang), north China (Inner Mongolia), northeast China (Jilin and Heilongjiang), eastern Russia (South Primorye), and Japan (Imo, Kamiyasse, Matsukawa and Ogatsu in the South Kitakami Belt, Moribu and Ise in the Hida Gaien Belt, Takauchi in the Maizuru Belt and Akasaka in the Mino Belt).

Order Orthotetida Waagen, 1884  
Suborder Orthotetidina Waagen, 1884  
Superfamily Orthotetoidea Wagen, 1884  
Family Derbyiidae Stehli, 1954  
Genus *Derbyia* Waagen, 1884

*Type species*.—*Derbyia regularis* Waagen, 1884.

*Derbyia* sp.

Figure 7.11

*Derbyia* sp. Tazawa, 2000, fig. 3.2.

*Material*.—One specimen, from locality HMF2, internal mould of a ventral valve, NU-B429.

*Remarks*.—This specimen is safely assigned to the genus *Derbyia* by its almost flat ventral valve, ornamented by numerous fine costellae and having a strong median septum 10 mm long. However, the single imperfect specimen does not allow specific assignment.

Order Orthida Schuchert and Cooper, 1932  
Suborder Dalmanellidina Moore, 1952  
Superfamily Enteletoidea Waagen, 1884  
Family Enteletidae Waagen, 1884  
Genus *Enteleles* Fischer de Waldheim, 1825

*Type species*.—*Enteleles glabra* Fischer de Waldheim, 1830.

*Enteleles* sp.

Figure 7.10a, 7.10b

*Enteleles* sp. Tazawa, 2000, figs. 3.1a, 3.1b.

*Material*.—One specimen, from locality HMF1, internal mould of a ventral valve, NU-B430.

*Remarks*.—The single ventral valve specimen of Moribu is safely assigned to the genus *Enteleles* by its small size (length about 10 mm, width about 11 mm), rounded elliptical outline, and having a long median septum and a pair of thin, long, subparallel dental plates, both of them extending to the midvalve. Specific identification remains difficult due to the poor preservation of the specimen.

Order Rhynchonellida Kuhn, 1949  
Superfamily Stenosismatoidea Oehlert, 1887  
Family Stenosismatidae Oehlert, 1887  
Genus *Stenosisma* Conrad, 1839

*Type species*.—*Terebratula schlotheimii* von Buch, 1835.

*Stenosisma margaritovi* (Tschernyschew, 1888)

Figure 8.1a–8.4

*Camarophoria margaritovi* Tschernyschew, 1888, p. 355, figs. 1–3; Fredericks, 1924, p. 48, pl. 1, figs. 32–42; text-fig. 4.

*Camarophoria humbletonensis* Howse. Hayasaka, 1922a, p. 62, pl. 9, figs. 10–12; pl. 10, fig. 9; Hayasaka, 1966, p. 1226, text-figs. 6–8.

*Stenosisma humbletonensis* (Howse). Tazawa, 1976, pl. 2, figs. 9, 10; Minato *et al.*, 1979, pl. 66, figs. 6–8.

*Stenosisma gigantea* (Diener). Lee and Gu, 1976, p. 272, pl. 176, fig. 3; pl. 177, fig. 18; Lee *et al.*, 1980, p. 395, pl. 173, figs. 6, 8.

*Stenosisma margaritovi* (Tschernyschew). Licharew and Kotlyar, 1978, pl. 17, figs. 7a, b; Koczyrkevich, 1979b, p. 50, pl. 11, figs. 5, 6; Duan and Li, 1985, p. 120, pl. 43, figs. 5–8; Tazawa and Matsumoto, 1998, p. 9, pl. 2, figs. 1–5; Tazawa, 2000, fig. 3.5; Tazawa, Takizawa and Kamada, 2000, p. 10, pl. 1, figs. 7–11.

*Stenosisma gigantea elongatum* Lee and Su, in Lee *et al.*, 1980, p. 395, pl. 173, figs. 1, 2.

*Stenosisma purdoni* (Davidson). Lee *et al.*, 1980, p. 395, pl. 173, figs. 4, 5, 7.

*Material*.—Five specimens, from localities HMF2, 3: (1) external cast of a conjoined valve, NU-B431; (2) external casts of three ventral valves, NU-B432–434; (3) external cast of a dorsal valve, NU-B435.

*Description*.—Shell medium size for genus, longer than wide, with greatest width slightly anterior to midvalve; length 21 mm, width about 18 mm in the best preserved specimen (NU-B434). Ventral valve gently convex in lateral profile; umbo small; sulcus shallow; costae often bifurcating or intercalating anteriorly, numbering 7–9 on sulcus and 6–7 on each flank. Dorsal valve moderately convex in lateral profile, with low fold; costae numbering 8 on fold and 6–7 on each flank.

*Remarks*.—These specimens are poorly preserved but can be referred to *Stenosisma margaritovi* (Tschernyschew, 1888) by their narrow and elongate outline, shallow ventral sulcus and low dorsal fold, and rather numerous costae on both valves.

The shells, described and figured as *Stenosisma humbletonensis* (Howse, 1848) from the lower Kanokura Formation of the southern Kitakami Mountains (Hayasaka, 1922a, 1966; Tazawa, 1976; Minato *et al.*, 1979), are referred to *S. margaritovi* on the basis of their shallow sulcus, low fold, and many costae on both valves.

An elongate species, described as *Stenosisma gigantea* (Diener, 1897), *S. gigantea elongatum* Lee and Su, in Lee *et al.*, 1980, and *S. purdoni* (Davidson, 1862) from the Middle Permian of Jilin and Heilongjiang, northeast China and Jisu (Zhesi), Inner Mongolia (Lee and Gu, 1976; Lee *et al.*, 1980), may be conspecific with *S. margaritovi*.



*Stenosisma tetricum* Grant (1976, p. 185, pl. 50, figs. 9–28) from the Rat Buri Limestone of Ko Muk, southern Thailand is also close to *S. margaritovi* in size and outline, but the Thailand species is distinguished from the present species by its strong concentric laminae on both valves.

**Distribution.**—Middle Permian (Murgabian-Midian) of north China (Inner Mongolia), northeast China (Heilongjiang and Jilin), eastern Russia (South Primorye), and Japan (South Kitakami and Hida Gaien Belts).

Superfamily Rhynchoporoidea Muir-Wood, 1955  
Family Rhynchoporidae Muir-Wood, 1955  
Genus *Rhynchopora* King, 1865

**Type species.**—*Terebratula geinitziana* de Verneuil, in Murchison *et al.*, 1845.

***Rhynchopora* sp.**

Figure 8.5a–8.5c

*Rhynchopora* sp. Shi and Tazawa, 2001, p. 756, figs. 2.2a, b.

**Material.**—One specimen, from locality HMF1, internal mould of a conjoined valve, NU-B478.

**Remarks.**—This specimen is safely assigned to the genus *Rhynchopora* by its small size (length 10 mm, width 9 mm), pentagonal outline, fine simple costae and, in particular, the high dorsal fold which originates from midvalve, has 5 costae and is sharply incurved ventrally to form almost a square-shaped, flat anterior surface at the anterior margin. The Moribu specimen well resembles *Rhynchopora tchernyshevi* Koczyrkevich (1979a, p. 47, pl. 11, figs. 1–4), originally described from the lower Barabash Formation of South Primorye, in size and outline of the shell, and the number of costae on the dorsal fold. But accurate comparison is difficult for the poorly preserved specimen.

Order Athyridida Boucot, Johnson and Staton, 1964  
Suborder Retziidina Boucot, Johnson and Staton, 1964  
Superfamily Retzioidea Waagen, 1883  
Family Neoretziidae Dagis, 1972  
Subfamily Hustediinae Grunt, 1986  
Genus *Hustedia* Hall and Clarke, 1893

**Type species.**—*Terebratula mormonii* Marcou, 1858.

***Hustedia ratburiensis* Waterhouse and Piyasin, 1970**

Figure 8.6a–8.6c

*Hustedia ratburiensis* Waterhouse and Piyasin, 1970, p. 138, pl. 23, figs. 15–30; Grant, 1976, p. 241, pl. 66, figs. 1–69; pl. 67, figs. 51–58; Sun, 1991, p. 254, pl. 6, figs. 5–8; Yanagida and Nakomori, 1999, p. 118, pl. 32, figs. 11–16.

*Hustedia thailandica* Waterhouse and Piyasin, 1970, text-figs. 12, 13.

*Hustedia nakomorii* Yanagida, 1970, p. 79, pl. 14, figs. 9a–d.

**Material.**—Four specimens, from localities HMF1, 2, 5: (1) external moulds of two ventral valves, NU-B436, 437; (2) external mould of a dorsal valve, NU-B438; (3) internal

mould of a dorsal valve, NU-B439.

**Description.**—Shell small to medium for genus, suboval in outline, with greatest width slightly anterior to midvalve; length 9 mm, width 8 mm in the larger ventral valve specimen (NU-B436). Ventral valve moderately convex in both lateral and anterior profiles, without sulcus. External surface of ventral valve ornamented by simple, broad and rounded costae; 2 close-set costae medially and 3 pairs of costae laterally. Dorsal valve moderately convex in both profiles, having no fold, and ornamented by 3 costae medially and 3 pairs of costae laterally; costae originating at umbo except median costa, which commences a little below umbo; outer 2 pairs of costae curved towards posterolateral margins. Internal structure of dorsal valve obscure in the present material.

**Remarks.**—The Moribu specimens can be referred to *Hustedia ratburiensis* Waterhouse and Piyasin, 1970 by their external ornament, 2 close-set costae on median part of the ventral valve and 3 costae on median part of the dorsal valve, especially the median costa of the dorsal valve originating a short distance below umbo. This species was described and compared in detail by Waterhouse and Piyasin (1970), Yanagida (1970) and Grant (1976).

A single dorsal valve specimen, figured by Koizumi (1979, pl. 1, fig. 5) as *Hustedia indica* (Waagen, 1883) from the Kashiwadaira Formation of the Takakurayama area, Abukuma Mountains, northeast Japan, resembles closely *H. ratburiensis* in having a median costa originating slightly anterior to umbo.

**Distribution.**—Lower Permian (Artinskian) to Upper Permian (Dzhulfian) of north-central Thailand (Khao Hin King), southern Thailand (Khao Phrik, Khao Tok Nam and Ko Muk), and central Japan (Hida Gaien Belt).

Order Spiriferida Waagen, 1883  
Suborder Spiriferidina Waagen, 1883  
Superfamily Martinioidae Waagen, 1883  
Family Martiniidae Waagen, 1883  
Subfamily Martiniinae Waagen, 1883  
Genus *Martinia* McCoy, 1844

**Type species.**—*Spirifer glaber* Sowerby, 1820.

***Martinia* sp.**

Figure 8.7a, 8.7b

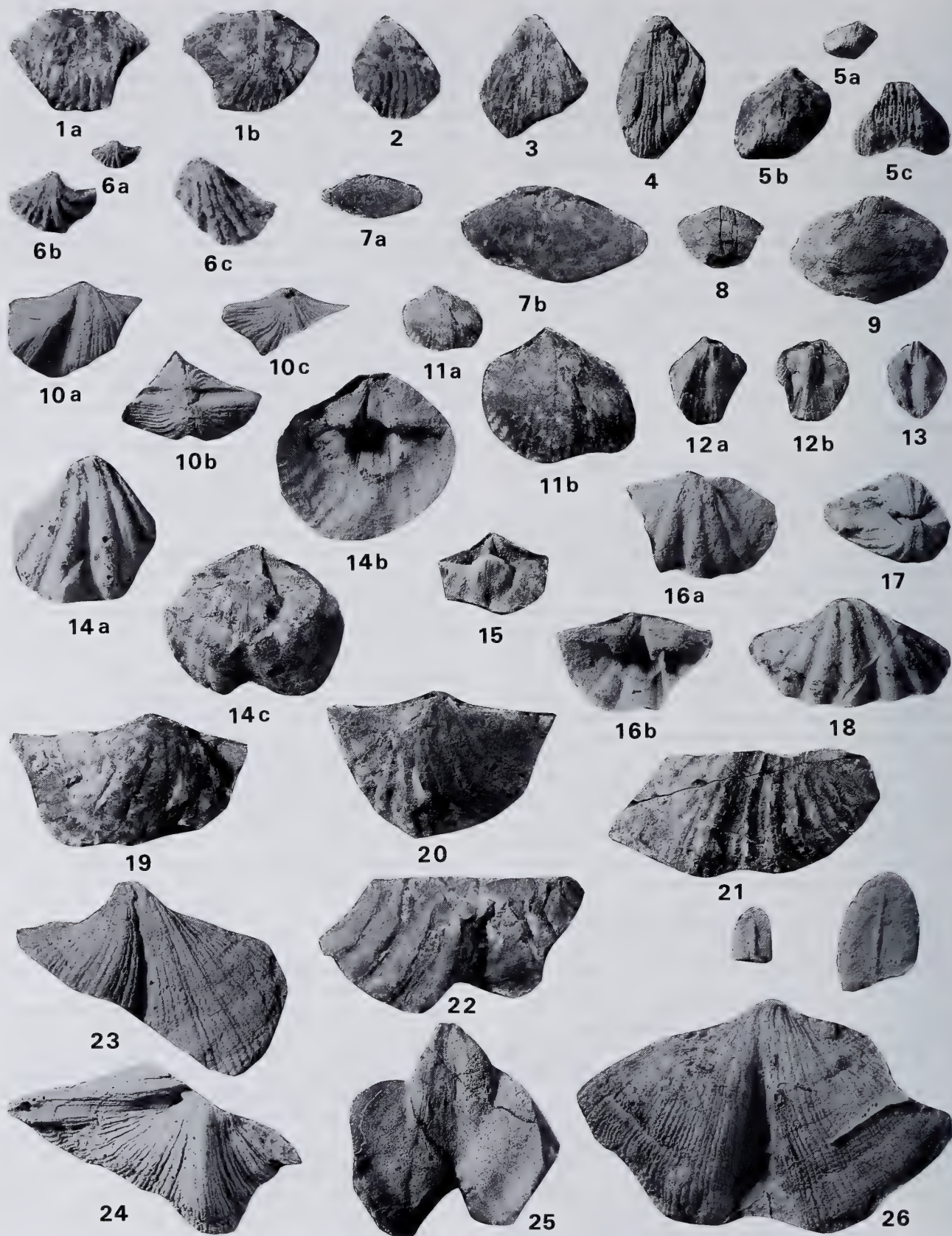
**Material.**—One specimen, from locality HMF3, internal mould of a ventral valve, NU-B440.

**Remarks.**—This specimen is safely assigned to the genus *Martinia* by its transversely subelliptical ventral valve with several vascular markings radially branching out from umbonal region and extending two-thirds of the length of the valve. However, the poor preservation of this specimen prevents accurate specific identification.

Family Martiniopsidae Kotlyar and Popeko, 1967  
Genus *Martiniopsis* Waagen, 1883

**Type species.**—*Martiniopsis inflata* Waagen, 1883.







***Martiniopsis* sp.**

Figure 8.8, 8.9

**Material.**—Two specimens, from locality HMF1, internal moulds of two ventral valves, NU-B441, 442.

**Remarks.**—These specimens are fragmentarily preserved, but safely assigned to the genus *Martiniopsis* by their transversely oval outline and a pair of long adminicula reaching to the midlength of the ventral valves. The Moribu species is a medium, transverse *Martiniopsis*; length about 21 mm, width about 28 mm in the larger specimen (NU-B441), and most resembles *Martiniopsis cathaysiensis* Grabau (1936, p. 242, pl. 21, figs. 7, 8; pl. 24, figs. 9a–e), from the Maping Limestone of Guangxi and Guizhou, south China, in size and shape of the ventral valve.

The single ventral valve specimen, described as *M. cathaysiensis* by Hayasaka (1967, p. 254, figs. 2a, b) from the lower Kanokura Formation of the southern Kitakami Mountains, is poorly preserved, and inadequate for comparison.

Superfamily Spiriferoidea King, 1846

Family Trigonotretidae Schuchert, 1893

Subfamily Neospiriferinae Waterhouse, 1968

Genus ***Neospirifer*** Fredericks, 1919

**Type species.**—*Spirifer fasciger* Keyserling, 1846.

***Neospirifer* cf. *fasciger*** (Keyserling, 1846)

Figure 8.10a–8.10c

**Compare.**—

*Spirifer fasciger* Keyserling, 1846 pars, p. 231, pl. 8, fig. 3b only; Chao, 1925, p. 236, pl. 3, figs. 1–2.

*Spirifer* (*Neospirifer*) *fasciger* Keyserling. Ozaki, 1931, p. 28, pl. 1, figs. 3–6.

*Neospirifer fasciger* (Keyserling). Archbold and Thomas, 1984 pars, figs. 1F, H, I, 2C only; Poletaev, 1997, pl. 4, figs. 2–7.

**Material.**—One specimen, from locality HMF8, external mould of a conjoined valve, NU-B443.

**Remarks.**—The material available is a single imperfect shell lacking the anterior and lateral parts. This specimen

is safely assigned to the genus *Neospirifer* because of its distinct fasciculate costae on the lateral slopes of both valves. Externally the Moribu specimen most resembles the shells of *Neospirifer fasciger* (Keyserling, 1846), described from the Upper Carboniferous of Gansu and Shanxi, north China and Jilin and Liaoning, northeast China (Chao, 1925; Ozaki, 1931). The lectotype of *N. fasciger*, designated by Cooper and Grant (1976, p. 2173) and refigured by Archbold and Thomas (1984, figs. 1F–I, 2C) and Poletaev (1997, pl. 4, figs. 3b–3d) is also close to the present specimen in size, outline and ornament of the brachial valve. The present material is, however, too imperfect for comparison.

Genus ***Blasispirifer*** Kulikov, 1950

**Type species.**—*Spirifer blasii* de Verneuil, 1845.

***Blasispirifer* cf. *reedi***

(Licharew, in Licharew and Kotlyar, 1978)

Figure 8.11a–8.13

*Spirifer* cf. *reedi* Licharew. Shi and Tazawa, 2001, p. 756, figs. 2.4–6.

**Material.**—Three specimens, from localities HMF1, 3: (1) internal mould of a conjoined valve, NU-B479; (2) internal mould of a ventral valve, NU-B480; (3) internal mould of a dorsal valve, NU-B481.

**Description.**—Shell small for genus, slightly transverse, rounded rhomboidal in outline, with narrow hinge; length 13 mm, width 14 mm in a dorsal valve specimen (NU-B481). Ventral valve with a narrow and deep sulcus. Dorsal valve having a narrow but distinct fold; costae mostly simple, but weakly bundled in the innermost pair bounding fold; numbering 9–12 on each slope, 5–6 on fold in dorsal valve. Internally ventral valve lacking dental plates. Dorsal valve with no crural plates.

**Remarks.**—These specimens are safely assigned to the genus *Blasispirifer* by their small, rounded rhomboidal shell, fine, weakly bundled costae on dorsal valve, and lacking both dental plates and crural plates. In size and shape, the Moribu specimens most resemble *Blasispirifer reedi*

← **Figure 8.** 1a–4. *Stenoscisma margaritovi* (Tschernyschew), 1a, 1b: Ventral and dorsal views of external cast of a conjoined valve, NU-B431, 2: External cast of a ventral valve, NU-B434, 3: External cast of a ventral valve, NU-B433, 4: External cast of a ventral valve, NU-B432, 5a–5c. *Rhynchopora* sp., dorsal and anterior views of internal mould of a conjoined valve, NU-B478, (5b, 5c x2), 6a–6c. *Hustedia ratburiensis* Waterhouse and Piyasin, 6a, 6b: External latex cast of a dorsal valve, NU-B438, (6b x2), 6c: External cast of a ventral valve, NU-B436, (x2), 7a, 7b. *Martinia* sp., internal mould of a ventral valve, NU-B440, (7b x2), 8, 9. *Martiniopsis* sp., internal moulds of two ventral valves, NU-B442, 441, 10a–10c. *Neospirifer* cf. *fasciger* (Keyserling), ventral, posterior and dorsal views of external latex cast of a conjoined valve, NU-B443, 11a–13. *Blasispirifer* cf. *reedi* (Licharew), 11a, 11b: Internal mould of a dorsal valve, NU-B481, (11b x2), 12a, 12b: Ventral and dorsal views of internal mould of a conjoined valve, NU-B479, 13: Internal mould of a ventral valve, NU-B480, 14a–14c. *Alispiriferella ordinaria* (Einor), external and internal latex casts and internal mould of a ventral valve, NU-B458, 15–18. *Alispiriferella japonica* sp. nov., 15: Internal mould of a ventral valve, NU-B462, 16a, 16b: External and internal latex casts of a ventral valve, NU-B461 (holotype), 17: Posterior view of external latex cast of a conjoined valve, NU-B460, 18: External latex cast of a ventral valve, NU-B465, 19–22. *Spiriferella lita* (Fredericks), 19: External cast of a dorsal valve, NU-B455, 20: External cast of a dorsal valve, NU-B452, 21: External cast of a dorsal valve, NU-B456, 22: External cast of a ventral valve, NU-B451, 23–26. *Gypsospirifer volatilis* Duan and Li, 23: External latex cast of a ventral valve, NU-B444, 24: External latex cast of a dorsal valve, NU-B449, 25: Internal mould of a ventral valve, NU-B448, 26: External latex cast of a ventral valve, NU-B445, 27, 28. *Dielasma* sp., external latex casts of two ventral valves, NU-B475, 474. (Natural size unless otherwise indicated).

(Licharew, 1978), originally described by Licharew (in Licharew and Kotlyar, 1978, p. 73, pl. 21, figs. 13a, b, v) from the Chandalaz Formation of South Primorye. Accurate comparison is difficult due to the lack of clear external information in the present material.

Genus **Gypospirifer** Cooper and Grant, 1976

*Type species.*—*Gypospirifer nelsoni* Cooper and Grant, 1976.

***Gypospirifer volatilis*** Duan and Li, 1985

Figure 8.23–8.26

*Gypospirifer volatilis* Duan and Li, 1985, p. 127, 207, pl. 48, figs. 1–2; pl. 49, figs. 1–2.

*Gypospirifer* sp. Tazawa, 2000, figs. 3.12, 3.13.

*Material.*—Seven specimens, from localities HMF5, 12, 25: (1) external moulds of a conjoined valve, NU-B444; (2) external moulds of three ventral valves, NU-B445–447; (3) internal mould of a ventral valve, NU-B448; (4) external and internal moulds of a dorsal valve, NU-B449; (5) external mould of a dorsal valve, NU-B450.

*Description.*—Shell medium to large for genus, transversely semielliptical in outline, with greatest width at hinge, and slightly alate; length 42 mm, width about 73 mm in the best preserved specimen (NU-B445).

Ventral valve gently convex in lateral and anterior profiles, most convex at umbonal region; umbo slightly extended and strongly incurved; sulcus very deep and rapidly widening anteriorly, with U-shaped bottom. External surface of ventral valve ornamented by numerous fine costae and concentric ornament of some rugae and numerous fine growth lines; costae subridged, added by bifurcation, and weakly fasciculated, numbering 9–10 in 10 mm at about midvalve, 7–8 in 10 mm at anterior margin. Dorsal valve gently convex in both profiles, having a high and narrow fold. External ornament of dorsal valve identical to opposite valve.

Ventral interior with a pair of thick, short dental plates and a deeply impressed, large, heart-shaped muscle field. Other internal structures not preserved.

*Remarks.*—These specimens are referred to *Gypospirifer volatilis* Duan and Li, 1985, originally described from the Middle Permian Zhesi (Jisu) Formation of the Zhesi area, Inner Mongolia, by their size, outline and surface ornament of shells, especially the deep ventral sulcus and high dorsal fold.

*Gypospirifer marcoui* (Waagen, 1883, p. 510, pl. 47, figs. 1–3) from the Amb and Wargal Formations of the Salt Range most resembles *G. volatilis*, but differs from the latter in having a shallower ventral sulcus and a lower dorsal fold.

The type species, *G. nelsoni* Cooper and Grant (1976, p. 2214, pl. 591, figs. 8–9) from the Hueco Formation of west Texas is clearly distinguished from *G. volatilis* by its more transverse shell, shallower ventral sulcus and lower dorsal fold.

*Distribution.*—Middle Permian (Murgabian) of north China (Inner Mongolia) and central Japan (Hida Gaian Belt).

Family Spiriferellidae Waterhouse, 1968  
Subfamily Spiriferellinae Waterhouse, 1968  
Genus ***Spiriferella*** Tschernyschew, 1902

*Type species.*—*Spirifer saranae* de Verneuil, 1845.

***Spiriferella lita*** (Fredericks, 1924)

Figure 8.19–8.22

*Spirifer saranae* mut. *lita* Fredericks, 1924, p. 36, pl. 1, figs. 16–27; Hayasaka, 1925, p. 98, pl. 5, fig. 14.

*Spiriferella lita* (Fredericks). Tazawa, 1979, p. 28, pl. 4, figs. 12–13; pl. 5, figs. 1–4, 6; Tazawa, 2000, fig. 3.9.

*Material.*—Seven specimens, from locality HMF2: (1) external cast of a ventral valve, NU-B451; (2) external mould and casts of three dorsal valves, NU-B452–454; (3) external casts of three dorsal valves, NU-B455–457.

*Description.*—Shell medium size for genus, transversely trapezoidal in outline; cardinal extremities blunt, produced; hinge straight, equal to widest part; length about 40 mm, width 68 mm+ in a dorsal valve specimen (NU-B457); length about 27 mm, width 43 mm in the best preserved dorsal valve specimen (NU-B452). Ventral valve having a deep, wide, V-shaped and smooth-bottomed sulcus and 5 strong, simple costae on each side of sulcus. Dorsal valve moderately convex in both lateral and anterior profiles, with a high fold and 5–6 simple or slightly bifurcated costae on each side of fold; fold having a median groove.

*Remarks.*—*Spiriferella lita* (Fredericks, 1924), originally described from the Middle Permian of Ussuri, South Primorye, is characterized by its strong and simple costae on the ventral valve, especially the enormously large costae on both sides of the sulcus. The material available consists of a fragmentarily preserved ventral valve and six incomplete dorsal valves. These specimens can be assigned to *S. lita* on account of their large, transverse shells with strong and simple costae on the ventral valve.

*Spiriferella keilhavi* (von Buch, 1846), from the Middle Permian of Bear Island, is also a large, transverse *Spiriferella*, but it differs from *S. lita* by its weakly fasciculate costae on both valves.

*Distribution.*—Middle Permian (Murgabian-Midian) of eastern Russia (South Primorye) and Japan (South Kitakami and Hida Gaian Belts).

Genus ***Alispiriferella*** Waterhouse and Waddington, 1982

*Type species.*—*Spiriferella ordinaria* Einor, 1939.

***Alispiriferella ordinaria***  
(Einor, in Licharew and Einor, 1939)

Figure 8.14a–8.14c

*Spirifer* (*Spiriferella*) *keilhavi* var. *ordinaria* Einor, in Licharew and Einor, 1939, p. 140, pl. 23, figs. 6, 7; pl. 24, figs. 1a–d.

*Spiriferella ordinaria* Einor. Nelson and Johnson, 1968, p. 738, pl. 95, figs. 5, 6; pl. 96, figs. 4–6; text-figs. 10, 13a; Bamber and Waterhouse, 1971, pl. 15, figs. 10, 12–14; Waterhouse *et al.*, 1978, pl. 2, figs. 6–8.



*Alispiriferella ordinaria* (Einor). Waterhouse and Waddington, 1982, p. 30, pl. 2, figs. 7–13; text-figs. 11i, j, 20; Abramov and Grigorjeva, 1988, p. 158, pl. 22, figs. 7a–g; pl. 25, figs. 4, 5; Shi and Waterhouse, 1996, p. 133, pl. 25, figs. 11–15; text-fig. 46.

**Material.**—Two specimens, from locality HMF12: (1) external and internal moulds of a ventral valve, NU-B458; (2) external mould of a dorsal valve with internal moulds of a conjoined valve, NU-B459.

**Description.**—Shell small to medium for genus, slightly wider than long, subpentagonal in outline, with greatest width at hinge; length about 31 mm, width about 37 mm in the better preserved specimen (NU-B458).

Ventral valve moderately convex in lateral profile, most convex at posterior third of shell length; cardinal extremities blunt, produced; interarea moderately high, triangular in shape and slightly concave; sulcus deep and having smooth, broad, V-shaped bottom; 4 pairs of broad, rounded, simple or bifurcated costae on ventral valve. Dorsal valve having a low fold, with a deep, wide, flat-bottomed median groove for almost entire length; 4 pairs of bifurcated or trifurcated costae on dorsal valve.

Ventral valve interior with a pair of high dental plates and a deeply impressed heart-shaped muscle field. Other internal structures not observed in the present material.

**Remarks.**—The Moribu specimens are not so well preserved but they can be identified with *Alispiriferella ordinaria* (Einor, 1939) by their small, slightly wider subpentagonal shell, with weakly bundled costae on both ventral and dorsal valves. This species was originally described by Einor (in Licharew and Einor, 1939) from the Lower Permian of Novaya Zemlya, and afterwards redescribed by Waterhouse and Waddington (1982) as the type species of the genus *Alispiriferella*.

**Distribution.**—Lower Permian (Asselian) to Middle Permian (Murgabian) of the Arctic Russia (Novaya Zemlya, western Verkhoyansk Range), northern Canada (Yukon Territory) and central Japan (Hida Gaian Belt).

*Alispiriferella japonica* sp. nov.

Figure 8.15–8.18

*Spiriferella* sp. Horikoshi *et al.*, 1987, p. 142; Tazawa, 1987, text-figs. 1.1, 1.3.

*Alispiriferella* sp. Tazawa, 2000, fig. 3.8.

**Material.**—Fourteen specimens, from localities HMF1, 2, 5, 8, 14, 16: (1) external mould of a conjoined valve, NU-B460; (2) external and internal moulds of three ventral valves, NU-B461 (holotype), 462, 463; (3) external moulds of eight ventral valves, NU-B464–471; (4) internal moulds of two dorsal valves, NU-B472, 473.

**Diagnosis.**—Small, transversely much wider *Alispiriferella* with alate cardinal extremities, smooth ventral sulcus and coarse, simple and rounded costae on both valves.

**Description.**—Shell small for genus, alate, transversely subquadrate in outline, with greatest width at hinge; length 21 mm, width 39 mm in the largest specimen (NU-B465); length 18 mm, width about 32 mm in the holotype (NU-B461).

Ventral valve strongly convex in lateral profile, most convex at umbonal region; umbo well extended and strongly incurved; interarea moderately high, nearly triangular in shape; cardinal extremities slightly produced; sulcus deep and wide, having smooth, rounded bottom; costae broad and simple with rounded crest, numbering 4–5 on each flank of ventral valve. Dorsal valve moderately convex in lateral profile; fold originating at beak and having a narrow but distinct median groove, which extends from umbo to anterior margin; each flank having 3–4 coarse, simple and rounded costae.

Ventral valve interior with high dental plates and a deeply impressed heart-shaped muscle field; the latter is longitudinally striated and divided into two parts by a low ridge with a median narrow groove. Dorsal valve interior obscure in the present material.

**Remarks.**—*Alispiriferella japonica* sp. nov. is distinguished from *Alispiriferella ordinaria* (Einor, 1939) by its more alate and wider outline, smooth noncostate ventral sulcus and coarse, simple costae on both valves.

The present species somewhat resembles *Alispiriferella* sp. Yanagida (1996, figs. 2.2, 2.4) from the Middle Permian Tsunemori Formation of Akiyoshi, southwest Japan in having transverse shell, broad, simple costae on both valves, and dorsal fold with a narrow median groove. The Akiyoshi species is unfortunately represented by only two incomplete specimens, and an accurate comparison is therefore hampered.

*Alispiriferella gydalensis* (Zavodowsky, 1968, p. 159, pl. 46, fig. 1) from the Middle Permian Omolon Horizon (correlated with the Kungurian) of the Kolyma River region, north-eastern Siberia, differs from *A. japonica* in having a much larger shell and dorsal fold with a wide, shallow median groove.

Order Terebratulida Waagen, 1883

Suborder Terebratulidina Waagen, 1883

Superfamily Dielasmatoidea Schuchert, 1913

Family Dielasmatidae Schuchert, 1913

Subfamily Dielasmatinae Schuchert, 1913

Genus *Dielasma* King, 1859

**Type species.**—*Terebratulites elongatus* Schlotheim, 1816.

*Dielasma* sp.

Figure 8.27, 8.28

**Material.**—Two specimens, from locality HMF3, external moulds of two ventral valves, NU-B474, 475.

**Description.**—Shell medium size for genus, elongate subpentagonal in outline, almost flat to slightly concave in both lateral and anterior profiles; length 29 mm, width 15 mm in the larger specimen (NU-B474). Ventral valve with narrow but distinct median fold, originating slightly anterior to umbo and extending to anterior margin. External surface of ventral valve smooth.

**Remarks.**—This species may be a new species of *Dielasma*. The Moribu species resembles *Dielasma* sp. B, described by Yang *et al.* (1962, p. 118, pl. 46, figs. 8a–c)

from the Middle (?) Permian of Qilianshan Mountains, Qinghai, northwest China, in size and shape of the ventral valve and in having a narrow, distinct median fold on the ventral valve.

*Dielasma biplex* Waagen (1882, p. 349, pl. 25, figs. 3–5) from the Wargal Formation of the Salt Range also has a narrow median ventral fold, but it is clearly distinguished from the *Moribu* species by its strongly convex ventral valve.

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# A phosphatized cephalopod mouthpart from the Upper Pennsylvanian of Oklahoma, U.S.A.

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**Abstract.** An exceptionally well-preserved cephalopod mouthpart was discovered in a phosphate concretion from the lower Missourian (Upper Pennsylvanian) in Tulsa, Oklahoma, U. S. A. It consists of an almost complete jaw apparatus and a radula, both of which are in the living orientation. The black upper and lower jaws, preserved as phosphate, were probably chitinous. The lower jaw is slightly larger than the upper and is characterized by a widely open outer lamella. The upper jaw is built up of a large outer lamella and a short, scallop-shaped inner lamella; the former is distinctly divided into two portions in the posterior region. The radula is preserved in the anterior portion of the buccal cavity; it is made of more than ten rows of teeth, each consisting of seven tooth elements with a pair of marginal plates. The overall features of the jaws and radula are essentially similar to those described in association with ammonoids rather than nautiloids and coleoids, suggesting that this mouthpart can be referred to the Ammonoidea. However, the lower jaw in our specimen differs from previously described mandibles of Carboniferous *Gastrioceratoidea*, *Neoglyphioceratoidea*, *Gonioloboceratoidea*, and *Dimorphoceratoidea* in its less elongate outline. For this reason, we refer the cephalopod mouthpart to the Ammonoidea other than the above superfamilies with reservation.

**Key words:** Ammonoidea, cephalopod mouthpart, Oklahoma, Upper Pennsylvanian

## Introduction

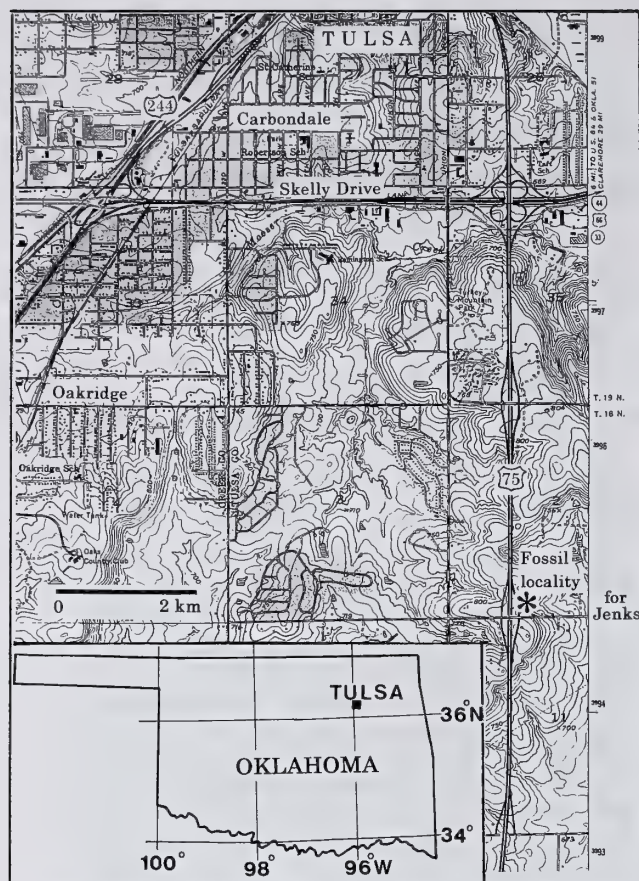
All extant cephalopods possess a well-developed buccal mass in the proximal portion of the digestive system. The organic hard tissues of the cephalopod buccal mass consist of upper and lower jaws (beaks or mandibles) and a radula, all of which are surrounded by well-developed jaw-radular musculature. Fossilized remains of jaws and radula are rarely found in body chambers of ectocochliate cephalopod shells, especially of ammonoids and in the soft tissue remains of coleoids (see Tanabe and Fukuda, 1999, for a recent review). As Mapes (1987) has briefly documented, the marine Carboniferous in the U.S. Midcontinent occasionally yields goniatite conchs preserving jaws and a radula within their body chambers (Saunders and Richardson, 1979; Tanabe and Mapes, 1995; Doguzhaeva *et al.*, 1997). These goniatites occur in carbonate and phosphate concretions, together with occasional isolated cephalopod jaws and even more rarely radulae. In this article, an exceptionally preserved cephalopod mouthpart from the Upper Pennsylvanian of Oklahoma is described and its possible

taxonomic relationship is discussed on the basis of comparison with the jaws and radulae of extant and fossil cephalopods.

## Material and its geologic setting

The cephalopod mouthpart examined was preserved as a nucleus in a small spherical phosphate concretion (ca. 15 mm in diameter) that was recovered by one of us (RHM) from the Lower Missourian (Upper Pennsylvanian) on the southern side of Tulsa, Tulsa County, Oklahoma. The concretion came from an approximately 3 m thick stratigraphic sequence that consists of three distinct black platy shales that were exposed at the northeast corner of the junction of the 71st Street and the U.S. Highway 75 in the southern part of Tulsa, Tulsa County, Oklahoma (SW1/4, SW1/4, sec. 2, T. 18 N., R. 12E.: Supulpa 71/2 minute quadrangle; Figure 1). These shales were deposited in marine water under oxygen-stressed conditions that occurred during three distinct times of marine transgression and regression (Boardman, personal commun., 2001). The stratigraphic





**Figure 1.** Index map of the southern part of Tulsa, Oklahoma, showing the locality of the cephalopod mouthpart remain examined.

assignment by Boardman *et al.* (1995, see localities OKM-28 and 56, p.86, although the reported coordinates they provide are incorrect) places these shale units in the lowest three cycles of the basal Missourian in the northern Midcontinent. All of the shales belong to the Coffeyville Formation, and the stratigraphic assignments for the three shale beds from oldest to youngest are the basal Tacket Shale, the lower Tacket Shale (= Mound City Member, Hertha Formation of Kansas) and the upper Tacket Shale (= Huspuckney Member, Swope Limestone of Kansas).

The exposure originally extended laterally for about 100 m and was covered by thousands of phosphate concretions that were eroding from the three black platy shales. Initial collections were made of the loose specimens on the surface without regard to stratigraphic position. In about 1990, prior to a field expedition to recollect and sample the exposure stratigraphically, the Oklahoma Highway Department of Transportation grassed the exposure, and it is not collectable at this time.

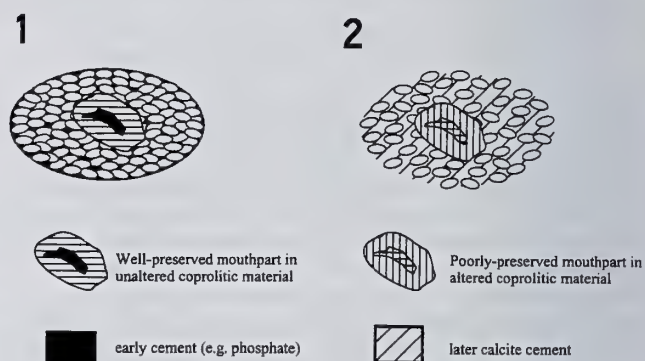
The cephalopod mouthpart specimen examined is housed in the Zoological Collection of Ohio University (OUZC).

### Notes on preservational conditions

It has been reported that some phosphate concretions from some Carboniferous Midcontinent black shales contain both mineralized skeletal material (bones and shells) and less commonly preserved softer organs (cephalopod mouthparts) of invertebrates (for mouthpart reports see Closs, 1967; Mapes, 1987; Tanabe and Mapes, 1995; Dogushaeva *et al.*, 1997). The reasons why and how phosphate preserves the soft tissue remains in this geologic setting has not been addressed. Because of the lack of *in situ* phosphate concretions from this Oklahoma locality, a detailed study of these specimens to solve the above problems is not warranted at this time. However, it is possible to make some general exterior and internal observations about the concretions from this exposure to help explain the preservation.

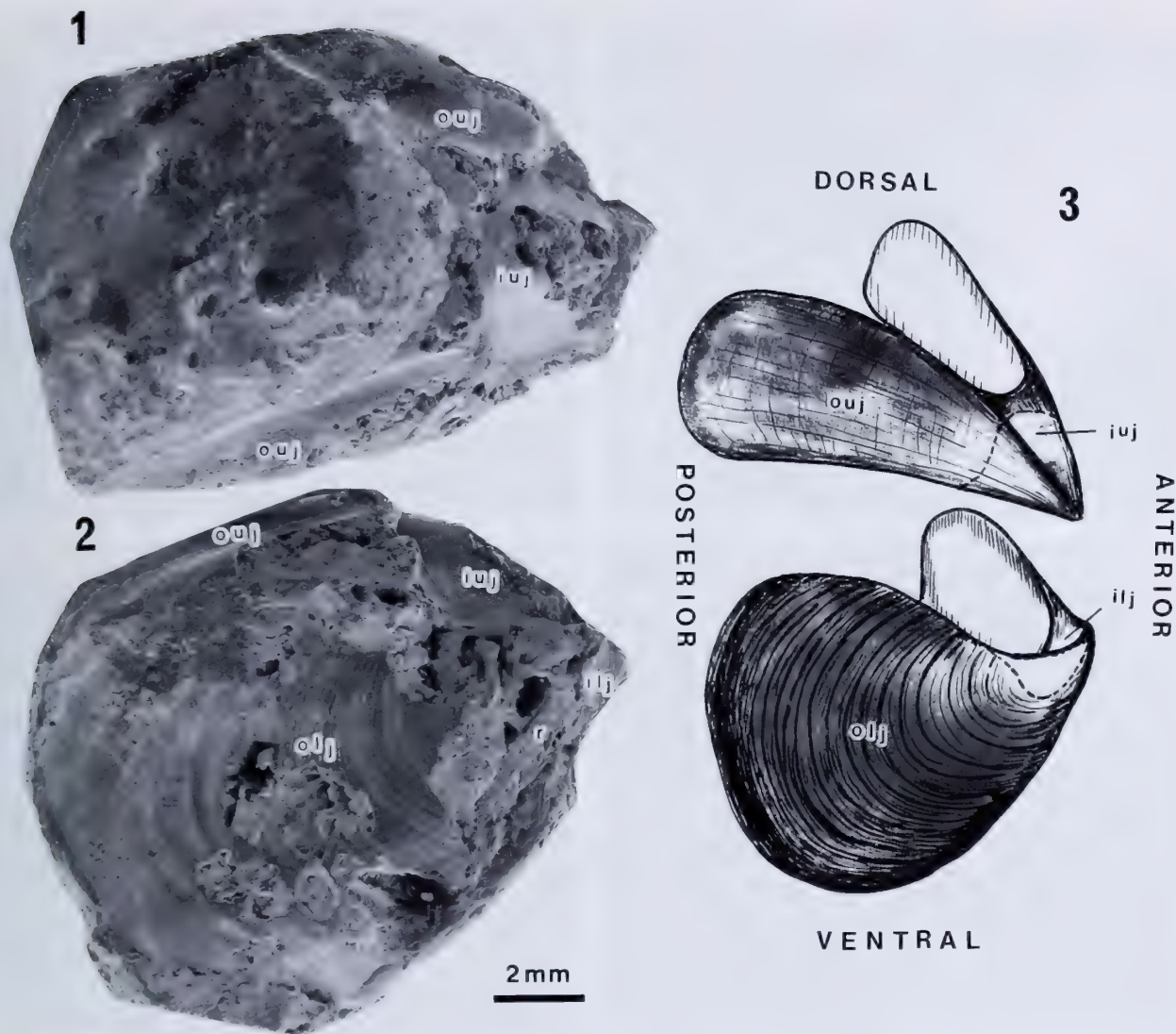
There are five concretion types classified on the basis of shape (flat and spheroidal) and on surface texture (smooth, rough, and bioturbated). The five concretion types are: 1) spheroidal with a smooth exterior, 2) flat with a smooth exterior, 3) spheroidal with a rough exterior, 4) flat with a rough exterior, and 5) bioturbated nodules which bear no body fossils. The cephalopod mouthparts that form the basis of this paper and most of the fossil material from this locality are preserved in the type 1 concretions. Although no systematic characterization of the nodule types was linked to the outcrop stratigraphy during initial collections in the early 1990s, the lowest shale (basal Tacket Shale Member) appeared to contain the most fossiliferous concretions.

The internal fabric of the concretions probably controls the surface texture and one of these fabrics lent itself particularly well to fossil preservation. Fecal pellets are common in these coprolite-dominated phosphate nodules. Both of the smooth-surfaced concretions (types 1 and 2) have a tightly packed, pelletal fabric without interstitial calcite cement; whereas, the two rough-surfaced types contain loosely



**Figure 2.** Schematic illustration of pelletal coprolites. 1. Tightly packed pelletal fabric that was cemented early enough to favor high-quality fossil preservation. 2. Calcite-cemented and loosely packed fabric that resulted in a rough surface exterior. Relatively poor fossil preservation characterizes these concretions probably because of later calcite cement that precipitated with infiltration of fluids that altered the coprolite and its enclosed fossils.





**Figure 3.** Dorsal (1) and left lateral (2) views of the phosphatized cephalopod mouthpart examined, and the reconstructed diagram of the jaw apparatus (anterolateral view) (3). Ohio University Zoological Collection, OUZC 4001. Abbreviations. ouj: outer lamella of upper jaw, ilj: inner lamella of upper jaw, olj: outer lamella of lower jaw, ilj: inner lamella of lower jaw, r: radula.

packed pellets and conspicuous interstitial calcite cement. The tight packing of pellets probably resulted in part from rapid, early diagenetic phosphate cementation of these concretions that sealed the concretions and favored high-quality fossil preservation by restricting entry of later pore fluids (Figure 2.1). Softness of pellets may also be a preservational factor, but analysis for that is beyond the scope of this report. The calcite cementation and loose packing of the rough concretions which contain poorly preserved fossils are interpreted as the result of infiltration of later diagenetic fossil-altering fluids (Figure 2.2).

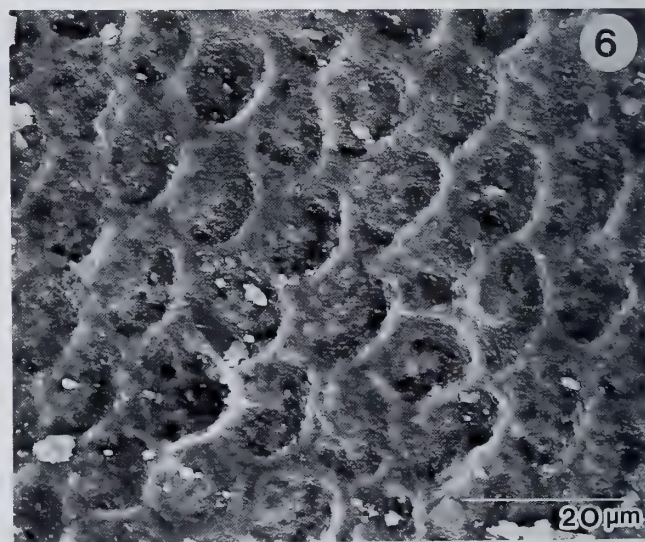
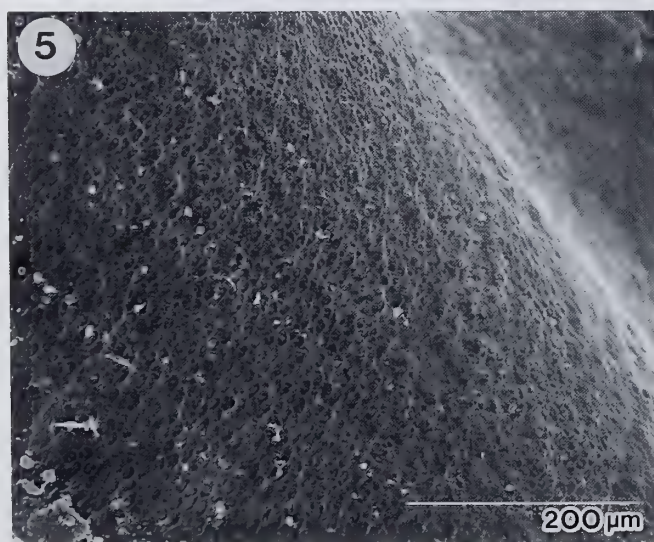
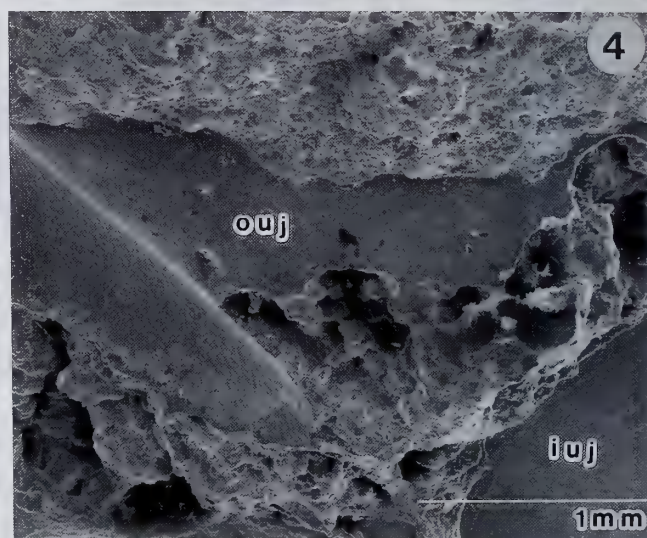
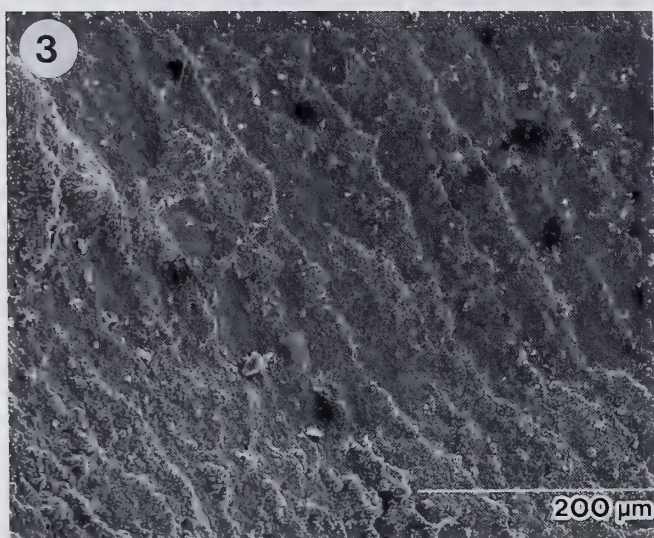
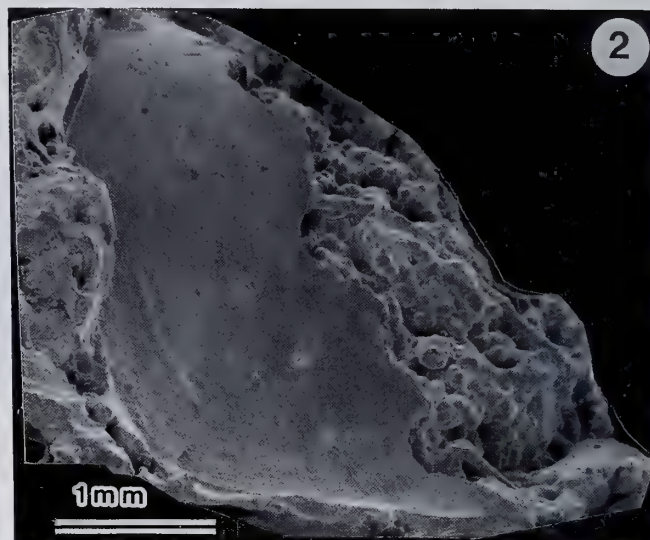
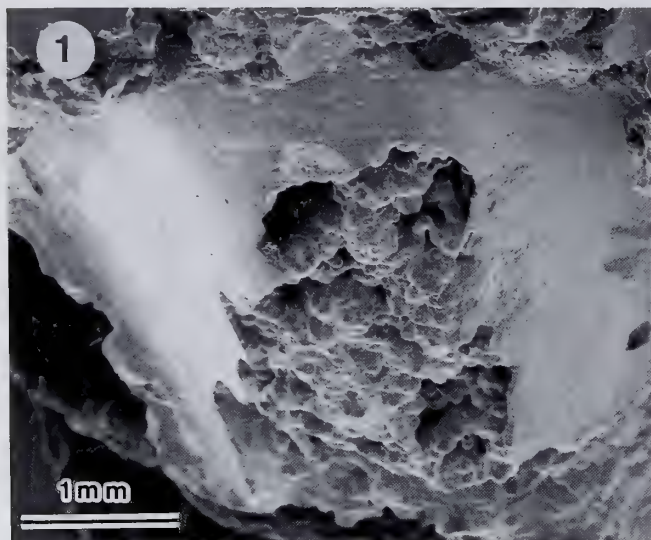
Based on these observations, it seems apparent that the mode of phosphate and carbonate preservation will control some of the preservational potential of cephalopod mouthparts. However, detailed studies of carefully collected

concretions will be required to resolve some of these preservational variables.

#### Description of the cephalopod mouthpart

*Methods of observations.*—The cephalopod mouthpart from the Tacket Shale (Tacket specimen) was coated with platinum and examined by means of a Hitachi model S2400 scanning electron microscope. SEM images of the jaws and radula were transferred to a desktop computer via a PCI interface, and different portions of them were reorganized into a few images using imaging software (Quartz PCI and Adobe Photoshop, Ver. 5). They were printed out using a high-resolution digital photo-printer (Fuji Film Pictography, model 3500).







For determination of upper and lower jaws, we follow the criteria described by Lehmann (1976, 1990), Nixon (1988a, 1996), and Tanabe and Fukuda (1999), who relied upon the comparison with the jaws of extant cephalopods.

**Overall morphology.**—The Tacket specimen, of about 11.5 mm maximum length and 7 mm width, consists of an almost complete jaw apparatus and a radula (Figure 3.1, 3.2). The ventral margin of the upper jaw fits well with the dorsal margin of the lower jaw. The anterior portion of the lower jaw is partly eroded and/or corroded, and where the mandible is missing, a radular ribbon is exposed in the buccal cavity between the jaws (*r* in Figure 3.2). These observations indicate that the jaws and radula have been fossilized by keeping their original life orientation as a complete buccal mass.

**Upper jaw.**—The upper jaw is made of a black material which was probably originally chitinous. It consists of a large outer lamella and a short inner lamella, which are joined in the anterior portion; the former, though the anterior portion is missing due to weathering, is distinctly divided into two wing portions in the posterior region (Figure 3.1). The open angle of the wings is about 45°. The dorsal margin of the paired wing portions exhibits a sharp ridge-like elevation. This elevation can be traced to the anterior portion where two wing portions are connected by a slightly concave outer lamellar element (Figure 4.4). The inner shorter lamella is scallop-shaped and is prominently convex dorsally (Figure 4.1, 4.2). The anterior portion is partly missing, but the reconstructed outline suggests that this portion appears to be sharply pointed (Figure 3.3). The inner lamella is ornamented with dense concentric lirae (Figure 4.1–4.3). The outer lamella lacks growth lines and instead retains a delicate pattern represented by numerous honeycomb-like polygonal pits (Figure 4.5, 4.6). Each pit, about 8–12 µm diameter, is surrounded by a sharp ridge (Figure 4.6). In view of their shape and distribution, these pits are undoubtedly comparable to the anchor-type polygonal imprints of columnar cells (becublasts) that are present on the outer side of the upper jaw and on the inner side of the lower jaw in extant coleoids (Dilley and Nixon, 1976).

**Lower jaw.**—As in the upper jaw, the lower jaw is made of a black, probably originally chitinous material without any trace of a calcareous element. It is slightly larger than the upper jaw (Figure 3.2), and consists of a large outer lamella and a short inner lamella, though the inner one is partly visible from outside in the eroded anterior buccal cavity (*ilj*; Figures 3.2, 3.3). The two lamellae are connected to each other in the anterior portion. The outer lamella is curved posteriorly, with an open angle of about 50 degrees. Its outer surface is sculptured by regular-spaced, concentric undulations, which become finer and denser toward the posterior margin (Figure 3.2).

**Radula.**—The exposed radula comprises a total of 13

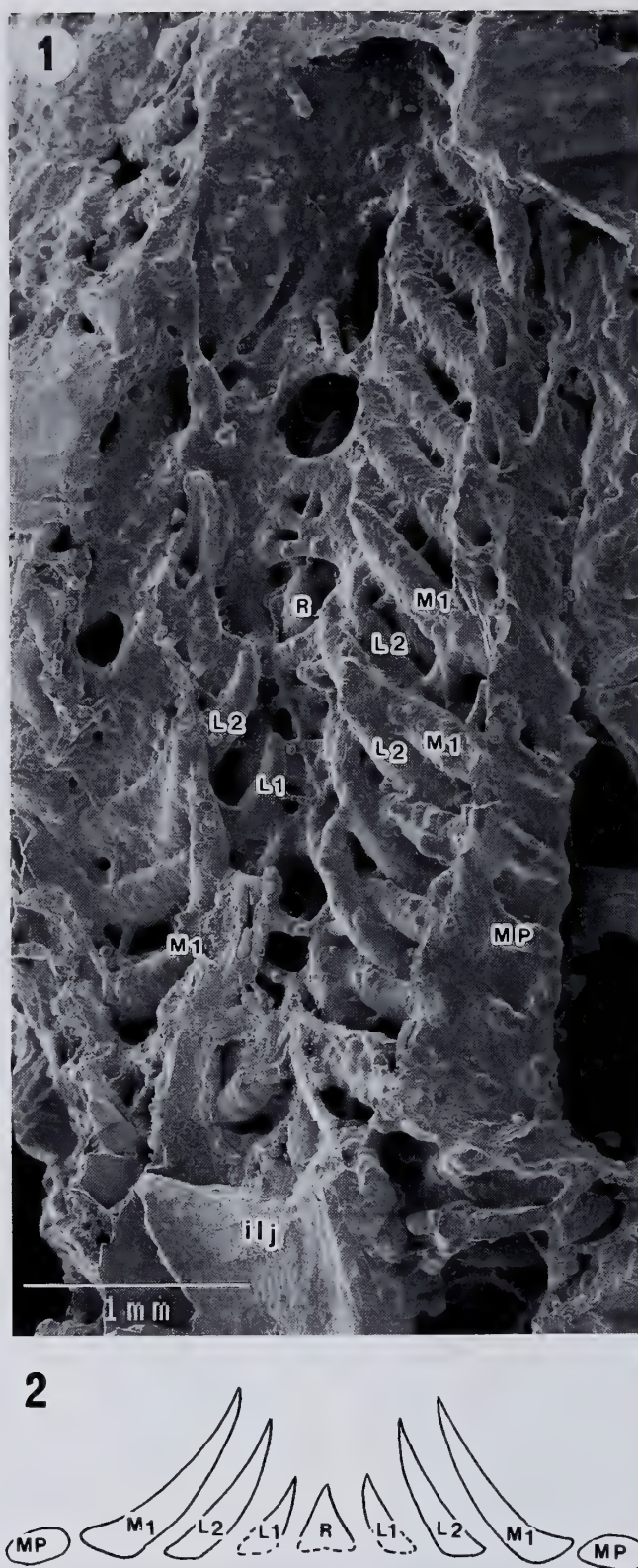
rows of teeth, retaining their original orientation. Each transverse row, about 2.5 mm wide, consists of seven tooth elements (a central rachidian tooth, two paired lateral teeth, and a pair of marginal teeth), with a pair of marginal plates (Figures 5.1, 5.2). The shape of the rachidian tooth is unclear because it is hidden by lateral teeth. The paired inner and outer lateral teeth are unicuspid, asymmetrical in frontal view and project markedly toward the anterodorsal side; the former is much shorter than the latter. The paired marginal teeth are the longest in the tooth elements and unicuspid as are the lateral teeth. The marginal plate has an oval outline.

### Taxonomic relationships

The isolated cephalopod mouthpart from the Tacket Shale exhibits several characteristic features including 1) a radula consisting of a total of seven tooth elements in each row, 2) an upper jaw being build up of a short, scallop-shaped inner lamella and a large outer lamella that is distinctly divided into two portions in the posterior region, 3) a lower jaw being made of a widely open outer lamella and a shortly reduced inner lamella, 4) absence of a calcareous jaw element, and 5) presence of coleoid-type polygonal imprints of beccublasts on the upper jaw lamella. These observations provide a reliable basis to infer the taxonomic relationship of the mouthpart owner by comparison with the radulae and jaws of extant and fossil cephalopods (Table 1). The upper jaw in our specimen is distinguished from those of extant coleoids and *Nautilus* in that the outer and inner lamellae of the latter are never divided into two wing portions (Clarke, 1986; Nixon, 1988a, b; Tanabe and Fukuda, 1999). Among the extant and fossil cephalopods, upper jaws with paired lamellae are only known from ammonoids (Tanabe and Fukuda, 1999, fig. 19.3). The three-dimensional architecture of the upper jaws of *Goniatitina* and *Ceratitina* is still unclear due to relatively poor fossil preservation. Bandel (1988, fig. 6) and Zakharov (1974, fig. 2B), respectively, reconstructed the upper jaws of the Upper Paleozoic goniatite (*Eoasianites*) and the early Triassic ceratite (*Olenekites*), as consisting of a widely opened, well-developed outer lamella and a short, reduced inner lamella. Later, Doguzhaeva *et al.* (1997) interpreted that the upper jaw of *Girtyoceras* (Carboniferous *Goniatitina*) is made of a large inner lamella and a short outer lamella, though they did not present an illustration showing this construction. The structure of the upper jaw in the Tacket specimen correlates well with the reconstruction of the upper jaws of goniatites and ceratites by Bandel (1988) and Zakharov (1974). Unlike the upper jaws of *Goniatitina* and *Ceratitina*, those of most Jurassic and Cretaceous ammonoids consist of a large inner lamella with paired lateral walls and a short, reduced outer lamella, though the two lamellae appear to be united as a single lamella in Late Cretaceous *Ancyloceratina* (e. g. *Jeletzkytes*;

← **Figure 4.** Upper jaw of the phosphatized cephalopod mouthpart examined. 1, 2: Anterior (frontal) (1) and right lateral (2) views of the scallop-shaped short inner lamella with concentric fine lirae. 3: Closeup of 2, showing the fine concentric lirae. 4: Part of anterior portion showing the outer lamella (*ouj*) with a strong lateral ridge and marginal portion of the inner lamella (*ijj*). 5: Outer surface of the left lateral portion of the outer lamella ornamented with numerous honeycomb-like imprints of beccublasts. 6: Closeup of imprints of beccublasts on the jaw plate, each surrounded by a sharp ridge.





**Figure 5.** 1. Anterior view of the radular ribbon preserved in the buccal cavity which is partly covered with the inner lamella of the lower jaw (ilj). 2. Diagram showing the frontal view of a transverse row of the radula. Abbreviations. R: central rachidian tooth, L1: inner lateral tooth, L2: outer lateral tooth, M1: marginal tooth, MP: marginal plate.



**Table 1.** Comparison of the morphological features of buccal structure in extant and fossil cephalopods (modified from Tanabe and Fukuda, 1999).

Cephalopod taxa	Upper jaw elements		Lower jaw elements			Beccublast imprints	Radular teeth in each row
	Rostrum	Lamellae	Rostrum	Inner lamella	Calcite cover		
Recent <i>Nautilus</i>	calcified	non-divided	calcified	shortly reduced	partly present	micropores	9
Recent Coleoidea	non-calcified	non-divided	non-calcified	projected posteriorly	absent	polygonal pits	7
<b>Ammonoidea</b>							
Goniatitina	non-calcified	divided	calcified?	shortly reduced	absent	polygonal pits	7
Ceratitina	non-calcified	divided	non-calcified	shortly reduced	absent	unknown	unknown
Phylloceratina	unknown	unknown	calcified	shortly reduced	absent	unknown	unknown
Lytoceratina	unknown	unknown	calcified	shortly reduced	absent	polygonal pits	unknown
Ammonitina	non-calcified	non-calcified	non-calcified	shortly reduced	present or absent	polygonal pits	7
Ancyloceratina	non-calcified	non-calcified	non-calcified	shortly reduced	present	unknown	7
Present specimen	non-calcified	non-calcified	non-calcified	shortly reduced	absent	polygonal pits	7

Landman and Waage 1993, figs. 37, 39–41; *Subptychoceras*; Tanabe and Landman, 2001, text-fig. 2. 6).

The lower jaw of the Tacket specimen is similar in the development of a large outer lamella to those of Upper Paleozoic Goniatitina such as *Eoasianites* (Neioceratoidea, Neioceratidae; Closs, 1967, fig. 4; Bandel, 1988, fig. 6), *Cravenoceras* (Neoglyphioceratoidea, Cravenoceratidae; Mapes, 1987, fig. 3.3, 3.4; Tanabe and Mapes, 1995, figs. 2–2, 3), *Wiedeyoceras* (Gonioloboceratoidea, Wiedeyoceratidae; Saunders and Richardson, 1979, fig. 7), and *Girtyoceras* (Dimorphoceratoidea, Girtyoceratidae; Doguzhaeva *et al.*, 1997, fig. 4), but in the latter, the outer lamellae are much more elongated posteriorly than in the former (we follow Bogoslovskaya *et al.*, 1999 for higher taxonomy of each genus). The lower jaw of an indeterminate goniatite (not *Girtyoceras limatum* as reported in Doguzhaeva *et al.*, 1997, fig. 2C, D) possesses a calcified rostrum, but such calcification has not yet been observed in the lower jaws of other Goniatitina and the Tacket specimen.

The radula in the Tacket specimen is allied to those of Goniatitina (e.g. *Eoasianites*; Lehmann, 1976, fig. 72; Tanabe and Mapes, 1995, figs. 2–4, 4–2; *Cravenoceras*; Tanabe and Mapes, 1995, figs. 2–3, 4–1; *Girtyoceras*; Doguzhaeva *et al.*, 1997, figs. 5A, 6A) in the number of tooth elements in each row and the overall shape of each tooth, though there are some variations in the relative length of marginal and lateral teeth. Also, polygonal imprints of beccublasts observed in the upper jaw of our specimen have been found on the upper jaw lamella of *Girtyoceras* (Doguzhaeva *et al.*, 1997, figs. 5B) as well as on the inside surface of the lower jaws of *Gaudryceras* (Cretaceous Lytoceratina; Tanabe and Fukuda, 1983, figs. 2, 3) and an unidentified aspidoceratid (Upper Jurassic Ammonitina; Tanabe and Fukuda, 1999, fig. 19.5D).

To summarize the above comparison, the overall features and structure of the jaws and radula in the Tacket specimen show an affinity to those described from the Upper Paleozoic Goniatitina, although, there is a marked difference in the lower jaw shape of the Tacket specimen and other described

goniatite mandibles. Because of this difference in lower jaw shape, we refer the Tacket cephalopod mouthpart to the Ammonoidea and to a superfamily other than the Gastrioceratoidea, Neoglyphioceratoidea, Gonioloboceratoidea, and Dimorphoceratoidea with reservation.

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# Taxonomic and phylogenetic aspects of the shell ultrastructure of nine Cretaceous rhynchonellide brachiopod genera

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**Abstract.** The shell ultrastructure of nine Cretaceous rhynchonellide brachiopod genera was studied using SEM with the purpose of finding additional criteria for the taxonomy and phylogeny of Late Cretaceous rhynchonellides. The genus *Orbirhynchia* is characterized by a coarse fibrous basiliolidine type structure of the secondary shell. The genera *Cyclothyris*, *Cretirhynchia*, *Septatoechia*, *Belbekella*, *Lamellaerhynchia*, *Almerarhynchia*, *Burrirhynchia* and *Grasirhynchia* have a fine fibrous rhynchonellidine type structure. An outline of some diagnostic characteristics for each genus is presented. Some diagenetic alterations of the shell, such as silicification and recrystallization are also discussed.

**Key words:** Cretaceous, rhynchonellide brachiopods, shell ultrastructure, systematics

## Introduction

Over the last four decades the shell ultrastructure of brachiopods has been extensively studied in order to throw light on the process of biomineralization. Since the contributions of Williams (1968a,b), MacKinnon (1974), and Smirnova (1984) shell ultrastructure has been used as an additional criterion for taxonomic and phylogenetic purposes. Shell ultrastructure of some Mesozoic rhynchonellides has been sporadically studied since the 1970's: Triassic - by Dagys (1974), Michalik (1993); Jurassic - by Baker (1971), Kamyshan (1977, 1986), Kamyshan and Adel (1979), Taddei Ruggiero and Ungaro (1983); Lower Cretaceous - by Smirnova (1984).

The shell ultrastructure of Late Cretaceous rhynchonellide brachiopod genera is poorly known. For the first time Nekvasilova (1974) briefly mentioned differences in the mosaic elements between the Late Cretaceous genera *Orbirhynchia* Pettitt and *Cretirhynchia* Pettitt. A short summary on some Late Cretaceous representatives from the Lesser Caucasus was published by Ali-zade *et al.* (1981), but without any illustrations. Gaspard (1990a, 1990b, 1996 *etc.*) published some illustrations of the microstructure of several species of the genus *Cyclothyris* McCoy, with emphasis on the growth patterns and effects of diagenesis. Motchurova-Dekova (1992) reported preliminary results on the shell ultrastructure of the genera *Cyclothyris* and

*Orbirhynchia*. Recently the ultrastructure of some representatives of *Erymnaria* Cooper and the new genus *Costerymnaria* Motchurova-Dekova and Taddei Ruggiero was studied (Motchurova-Dekova and Taddei Ruggiero, 2000). The purpose of this paper is to describe the shell microstructure of additional Cretaceous rhynchonellide genera with emphasis on Late Cretaceous representatives. New characters are found, increasing the possibility of using shell microstructure as an additional criterion in taxonomy and phylogeny.

## Material and methods

A comparative ultrastructural SEM analysis has been carried out on nine Cretaceous rhynchonellide genera. Depending on the available material, some genera were investigated extensively (*Orbirhynchia*, *Cyclothyris*, *Cretirhynchia*, *Septatoechia*), while others were examined briefly for comparative purposes (*Belbekella*, *Lamellaerhynchia*, *Almerarhynchia*, *Burrirhynchia*, *Grasirhynchia*). This preliminary study aims at discerning only certain general features. More detailed results will be published later.

Of importance in any ultrastructural comparison is the need for consistency in the location of longitudinal and transverse sections of adult shells. The sections should be the same for all specimens in order to be able to compare the ultrastructural details between different specimens.



For the present study SEM analyses were carried out on fifty transverse shell sections from thirty-four specimens belonging to twenty-nine species of nine Cretaceous rhynchonellide genera. In most specimens usually only two very close transverse sections of both valves were observed for each specimen. The sections were cut perpendicular to the plane of symmetry. Following the recommendation of Sass and Monroe (1967) the sections were made at the maximum width of the valves. In some specimens one of the sections was made more posteriorly and crossed the muscle field. Longitudinal sections in the plane of symmetry, made before this study, gave only general information about the thickness of the shell and the calcitic layers along the shell length and the length of the fibres.

The primary layer was normally affected by diagenetic processes and/or was not well preserved. Thus the characteristics of the secondary layer were mainly used as diagnostic features. The measurements of the cross-sections of fibres were taken in the central part of the transverse section. Because the long axes of fibres are usually inclined to the shell surface at about 10°, the real values of the width and thickness of the fibres presented here could be slightly overestimated. This usually holds true for all measurements taken, so principally it should not affect the way of comparison because similar values are compared.

The longer axis in the cross-sections of the fibres, usually parallel to the shell surface, is the **width (W)** of the fibre; the shorter axis, perpendicular to the longer axis, is the **thickness (T)** of the fibre. A coefficient "**C**" is introduced here representing the ratio between the width and the thickness of the fibre in the cross-section. "**C**," is the ratio W/T in the larger fibres, which usually make up the main part of the shell. "**C**<sub>2</sub>" is the ratio W/T of the thinner fibres, usually building the outer or the innermost sublayer of fibres in the shell, or forming thin bands of finer fibres inside the section. The shape of the cross-sections of the fibres and the differentiation of the secondary layer were used as additional diagnostic criteria. The reported **W** and **T** values, measured at the central part of the maximum width section of each specimen, were compared. The range of their variation (lowest and highest values) was taken into consideration.

The following is a brief summary of the results. Detailed data about the occurrences of the mentioned species can be found in the cited references. When a species is first mentioned here, the name of the collection is given and open nomenclature is used in some cases. Abbreviations: NHM - Natural History Museum London; NMNHS - National Museum of Natural History-Sofia.

### Observations and results

All studied fossil rhynchonellides are impunctate and composed of two calcitic layers - primary microgranular and secondary fibrous (Figure 1A). The previously described tertiary prismatic layer in the genus *Cyclothyris* (Motchurova-Dekova, 1992, 1994) was not observed. Extensive SEM observations showed instead that a row of large calcite prisms, perpendicular to the internal surface was developed in many specimens. Though they look like a prismatic layer, they are a result of diagenetic calcite formation

(Figures 1B, 2A, D). Recrystallized diagenetic calcite prisms forming a pseudo-tertiary layer were also observed in lenses in the interior of the secondary layer (Figure 5B). Such extensive SEM observations of the diagenetic alterations of the shell and the observation of this type of pseudo "tertiary layer" which is a result of secondary diagenetic processes, call into question the report of a tertiary layer in some rhynchonellides.

The **periostracum** is rarely preserved in fossil material. Gaspard (1982) reported a remarkable preservation of the organic cover of the Cretaceous terebratulid *Sellithyris*. Casts of periostraca on the external shell surface of living and fossil brachiopods are more frequently found. In the course of the present study neither of the above states of preservation of the periostracum were observed. However, in a particular spot of a transverse section of *Cyclothyris difformis*, the primary microgranular layer is overlain by an extremely thin calcite layer, only 2–10 µm thick (Figure 1D–F). It could be possibly interpreted as a diagenetically formed calcitic pseudomorph on the organic periostracum.

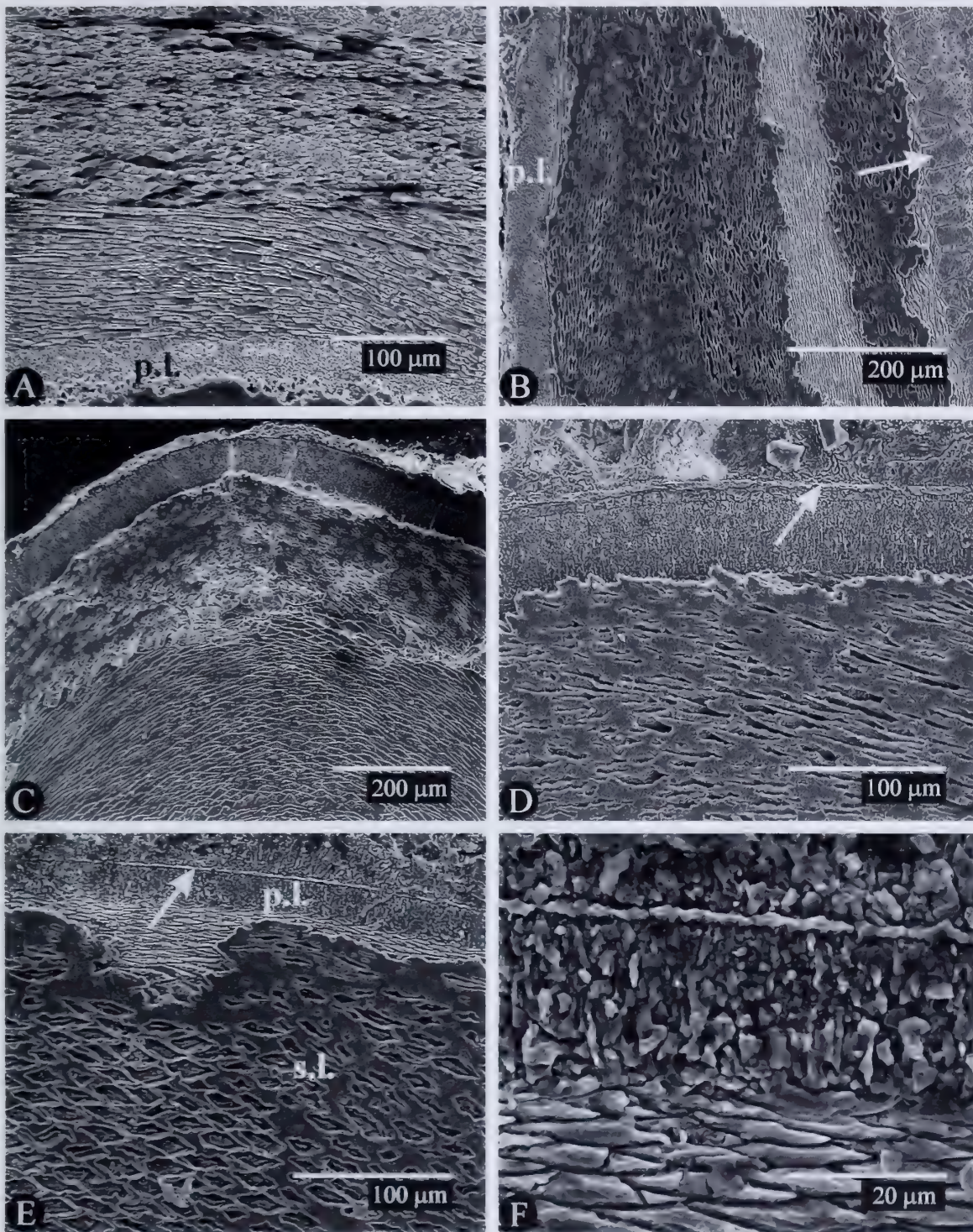
The **primary layer** is composed of isometric or elongate microgranular calcitic prisms perpendicular or slightly inclined to the shell surface. In most specimens the primary layer is fully or partly recrystallized (Figure 3F). It is interesting to note that in shells affected by strong silicification the primary layer is usually not silicified (Figure 1C, D). This is because the primary layer is not porous and is more compact than the fibrous layer when the organic sheets in the secondary layer are dissolved during early diagenesis.

The **secondary layer** is built up of fibres with long axes subperpendicular to the growth lines of the shell. The fibres display variable shapes in cross-section. The shape may be rhomboidal or parallelogram with variously outlined sides and angles (Figure 2E); or may have an anvil-like outline, formed by two arcs - larger and smaller, connected laterally by two sides; or the small arc can be missing (Figures 3F, 5D). Those species characterized by more isometric rhombic cross-sections of the fibres have lower values of the coefficient C, whereas species with fibres that are anisometric (elongate) anvil-like or rhombic in sections have higher values of C. In some specimens the secondary layer is strongly silicified (Figures 1B, 5F). When the silicification is not complete, siliceous pseudomorphs of the organic sheets are observed, representing a high relief silica grid enveloping the fibres (Figure 1E, 2E). In this case it is considered that the fibres, although recrystallized, have preserved their original shape.

### *Orbirhynchia* Pettitt, 1954

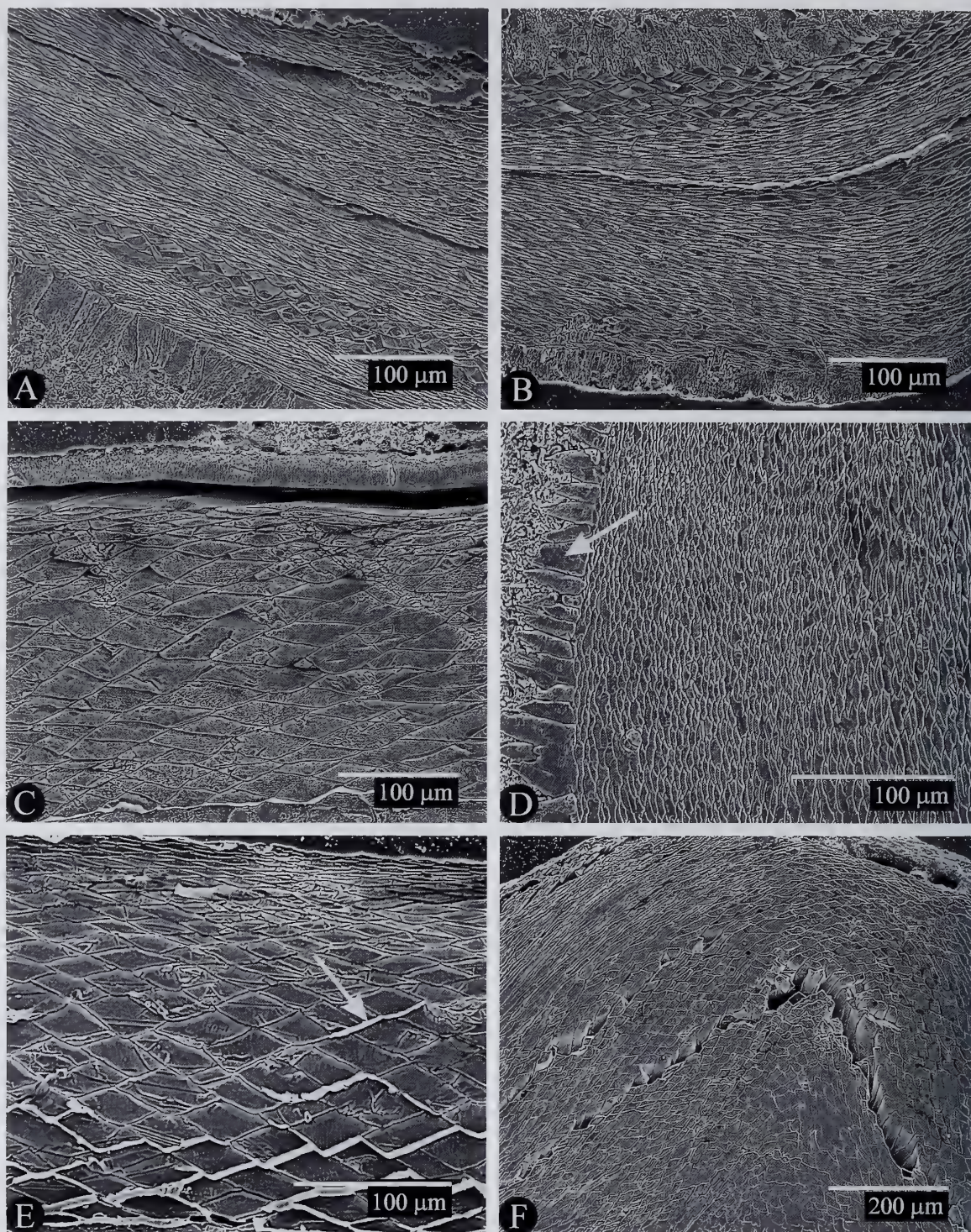
Seven species of *Orbirhynchia* were studied: *Orbirhynchia reedensis* (Etheridge), (Figure 2C), Upper Turonian, described in Nekvasilova (1974); *O. mantelliana* (J. de C. Sowerby), Middle Cenomanian (Coll. Eric Simon, Cran d'Ecailles); *O. aff. mantelliana*, *O. aff. boussensis* Owen (Figure 2E), *O. parkinsoni* Owen, *O. wiesti* (Quenstedt), Cenomanian (Motchurova-Dekova, 1996), and *Orbirhynchia* sp.1, Bulgaria, Lower Maastrichtian (Coll. NMNHS). The shell is relatively thin - 300–400 µm. The primary layer is rarely preserved, 20–40 µm thick and usually recrystallized. The secondary layer is built up of fibres that are anisometric





**Figure 1.** **A.** *Cyclothyris* aff. *difformis* (Valenciennes in Lamarck), Predboj near Prague, Czech Republic, Cenomanian, sample 18a. Transverse section through the whole shell thickness. p.l. - primary layer below, secondary layer differentiated. **B-F.** *Cyclothyris* *difformis* (Valenciennes in Lamarck) from Dobrevka chuka, NE Bulgaria, Cenomanian. **B** - sample 43a, section through the whole shell thickness; p.l. - primary layer on the left, not silicified, secondary layer partly silicified; arrow on the right-diagenetic calcite underlying the secondary layer. **C** - sample 42b, rib; primary layer above, recrystallized, but not silicified, secondary layer-partly silicified close to the primary layer. **D** - sample 42b, strongly silicified secondary layer-below and recrystallized, but non silicified primary layer above. The primary layer is overlain by a thin cover layer, supposed to be the calcitic pseudomorph of the periostracum - arrow. **E** - sample 43a, partly silicified secondary layer (s.l.) and non silicified primary layer (p.l.), covered by thin calcitic layer, probably a pseudomorph of the periostracum - arrow. **F** - close up of the area arrowed in E.





**Figure 2.** **A, B.** *Cyclothyrus antidichotoma* (Buvignier), Shenley Hill, Leighton Buzzard, Bedfordshire, England, Lower Albian, *L. regularis* Subzone. **A** – sample 13a, section through the whole shell thickness, primary layer missing. Internal shell surface in the lower left corner encrusted with diagenetic calcitic prisms. **B** – sample 13, Section through the whole shell thickness. Primary layer below, recrystallized. **C.** *Orbirhynchia reedensis* (Etheridge), Bohemia, Czech Republic, Upper Turonian, sample 21a. Whole shell thickness, primary layer above. **D.** *Burrirhynchia leightonensis* (Walker), Leighton Buzzard, Bedfordshire, England, Lower Albian, *L. regularis* subzone, sample 4a. Secondary fibres. Internal shell surface, vertical, on the left, overgrown by diagenetic calcite crystals (arrow), perpendicular to the surface. **E.** *Orbirhynchia* aff. *boussensis* Owen, Kaspichan, NE Bulgaria, Cenomanian, sample 37. Secondary layer, rhomboidal or parallelogramic fibres; siliceous pseudomorphs on the organic sheets in the lower half of the picture (arrow). **F.** *Cretirhynchia plicatilis sensu* Aliev and Titova, 1988, Lesser Caucasus, Russia, Coniacian-Santonian, sample 34b. Section through a rib, secondary layer.



in cross-section, representing well-shaped rhombi or parallelograms, with straight sides and well defined angles. Rarely the cross-sections of the fibres are anvil-like. The fibres are very large ( $W = 35\text{--}120\text{ }\mu\text{m}$ ,  $T = 10\text{--}50\text{ }\mu\text{m}$ ;  $C_1 = 1.1\text{--}4$ , usually 2–3). The stacking of the fibres is uniform. In some species thinner fibres are developed close to the external surface, passing gradually into larger fibres towards the internal part of the shell.

#### ***Cyclothyris* McCoy, 1844**

*Cyclothyris antidichotoma* (Buvignier), (Figure 2A, B), Lower Albian (Owen, 1962); *C. aff. difformis*, (Figure 1A), Cenomanian (Nekvasilova, 1973), *C. difformis* (Valenciennes in Lmk), (Figure 1B–F), Cenomanian (Motchurova-Dekova, 1996), *C. zahalkai* Nekvasilova, Lower Turonian, (Nekvasilova, 1973) and *C. vespertilio* (d'Orbigny), France, Santonian (Coll. NHM) were examined. The shell thickness is 300–350  $\mu\text{m}$  in *C. zahalkai* and *C. antidichotoma*, and reaches 700–1000  $\mu\text{m}$  in *C. difformis* and *C. vespertilio*. The primary layer is relatively thick in *C. aff. difformis* and *C. difformis*, reaching up to 20% (50–80  $\mu\text{m}$ ) of the total shell thickness. It is interesting to note that both species with thick primary layers inhabited a very shallow transgressive sea floor, namely the sublittoral zone near its boundary with the littoral zone (Nekvasilova, 1973). All species are characterized by the predominance of anisometric anvil-shaped (to rarely rhomboidal) fibres in the secondary layer, 15–30  $\mu\text{m}$  thick and 2–10  $\mu\text{m}$  wide.  $C_1$  is usually between 4 and 5, but can reach a maximum value of 8. The secondary layer is usually composed of several packages of fibres with different orientation, so that the distribution of the fibres is not uniform in any particular cross-section (Figure 1A). In *Cyclothyris antidichotoma* a band of distinctly more isometric fibres is noted near the interior of the shell (Figure 2B), which looks like fibres close to the anterior margin of muscle scar tissue.

#### ***Cretirhynchia* Pettitt, 1950**

The summary given below concerns only some species attributed to *Cretirhynchia* by different authors. The type species *Cretirhynchia plicatilis* (J. Sowerby) was not studied due to lack of material. The revision of this genus was still in progress during the preparation of this paper. In the recently published first step in the revision (Simon and Owen, 2001), the genus was split in four subgenera and one new genus was proposed. This probably could explain the variability in the shell ultrastructure of the studied species.

The thick-shelled species of *Cretirhynchia* constitute a group that is easily distinguished from the other representatives of *Cretirhynchia* (Motchurova-Dekova, 1993). In the current study these are *Cretirhynchia plicatilis sensu* Aliev and Titova, 1988 (Figure 2F) from Lesser Caucasus, Coniacian-Santonian (Aliev and Titova, 1988), *Cretirhynchia* sp. 1, Upper Campanian, and *Cretirhynchia* sp. 2 (Figure 3A), Lower Maastrichtian from Bulgaria (Coll. NMNHS). They seem to be close to the type species *Cretirhynchia plicatilis* (J. Sowerby). The three species studied here are characterized by thickening of the umbonal parts with callus, which blurs the outline of the internal morphology. The serial sections show strongly convergent dental plates, short

ventrally deflected hinge plates, simple subquadrate crural bases, and radulifer crura keeping close together anteriorly. However, their serial sections are more similar to the sections of *C. norvicensis* Pettitt, published by Owen (1962), than to the sections of *Cretirhynchia plicatilis* published by Pettitt (1950). The shell of the three studied species (*Cretirhynchia plicatilis sensu* Aliev and Titova, 1988; *Cretirhynchia* sp. 1 and *Cretirhynchia* sp. 2) is very thick: 1000–1800  $\mu\text{m}$ . Where preserved, the primary layer was strongly recrystallized, built up of acicular crystals perpendicular to the shell surface. The secondary layer is characterized by the prevalence of comparatively isometric fibres (Figures 2F, 3A), which have rhombic or rarely anvil-like outlines ( $W = 20\text{--}40\text{ }\mu\text{m}$ ;  $T = 15\text{--}25\text{ }\mu\text{m}$ ;  $C_1$  having lower values - 1.2 to 2.5, rarely reaching 3.5). In these species the anisometric fibres are usually confined to the outermost part of the shell, reaching higher coefficients  $C_2$  - up to 8–10 (Figure 3A).

According to Simon and Owen (2001), the group of species with the above mentioned internal details constitute the subgenus *Cretirhynchia* (*Cretirhynchia*). SEM investigations on the type species *Cretirhynchia plicatilis* (J. Sowerby) are also necessary to confirm the above remarks about the shell ultrastructure of the "true" *Cretirhynchia*.

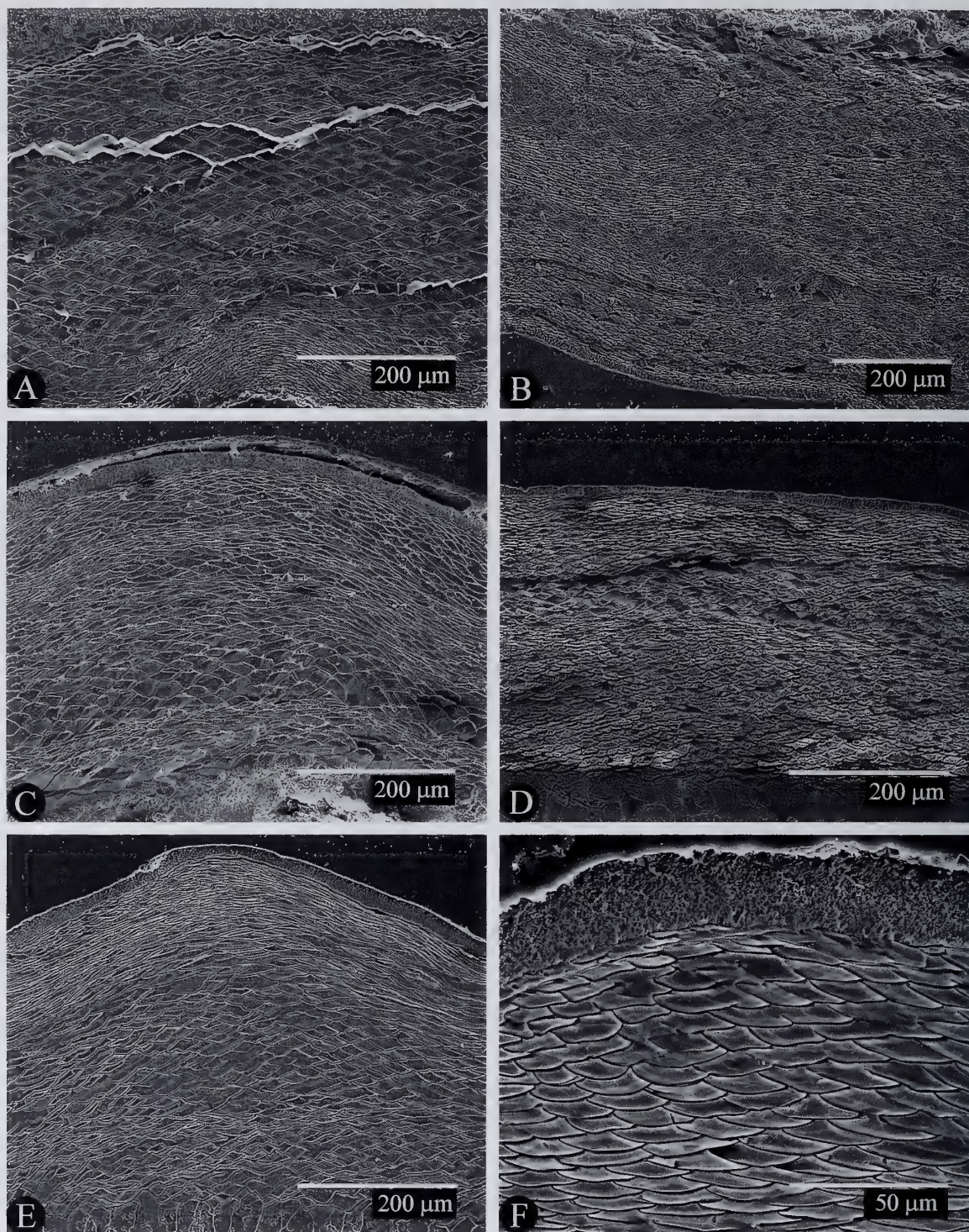
The remaining species attributed to the genus *Cretirhynchia* display a different fabric of shell ultrastructure.

The shell of *Cretirhynchia exsculpta* Pettitt, Lower Campanian (Pettitt, 1950) is 350–600  $\mu\text{m}$  thick. The primary layer is 30–40  $\mu\text{m}$  thick and composed of fine acicular calcite crystals, almost perpendicular to the shell surface. The pattern of the secondary layer is different in two sections at a distance of 2 mm. In the section posteriorly to the mid-line, two kinds of fibres are developed (Figure 3B): (1) more isometric ( $W = 25\text{--}50\text{ }\mu\text{m}$ ;  $T = 10\text{--}20\text{ }\mu\text{m}$ ;  $C_1 = 1.8\text{--}3$ ) and (2) more anisometric, ( $W = 40\text{--}65\text{ }\mu\text{m}$ ;  $T = 4\text{--}15\text{ }\mu\text{m}$ ;  $C_2 = 3\text{--}6$ ). The prevailing part of the fibres is rhombic to parallelogram, but some are anvil-like. The thinner fibres seem to be distributed in thin subparallel bands within the section, but recrystallization blurs the original pattern. The second section situated more anteriorly, shows monotonously arranged fibres with no obvious signs of recrystallization, although the bands of thinner (or differently oriented) fibres could also be noticed (Figure 3C).

*Cretirhynchia aff. cuneiformis*, Upper Turonian (Nekvasilova, 1974). Most probably this Bohemian species is quite distinct from *Cretirhynchia cuneiformis* Pettitt (1950), which has just been assigned as the type species of the new genus *Woodwardirhynchia* by Simon and Owen (2001). The maximum shell thickness in *Cretirhynchia aff. cuneiformis* is 370  $\mu\text{m}$ , the primary layer being 30  $\mu\text{m}$  thick and built up of acicular crystallites (Figure 3D). The secondary fibres have rhombic to anvil-like outlines. Relatively isometric fibres are sporadically distributed in bands or lenses ( $W = 25\text{--}38\text{ }\mu\text{m}$ ;  $T = 7\text{--}17\text{ }\mu\text{m}$ ;  $C_1 = 2\text{--}3.5$ ). The anisometric fibres prevail ( $W = 20\text{--}50\text{ }\mu\text{m}$ ;  $T = 3\text{--}14\text{ }\mu\text{m}$ ;  $C_2 = 3.5\text{--}6.5$ ). These peculiarities are reminiscent of *Cyclothyris*, but the fibres in *Cyclothyris* have a maximum of 40  $\mu\text{m}$  width.

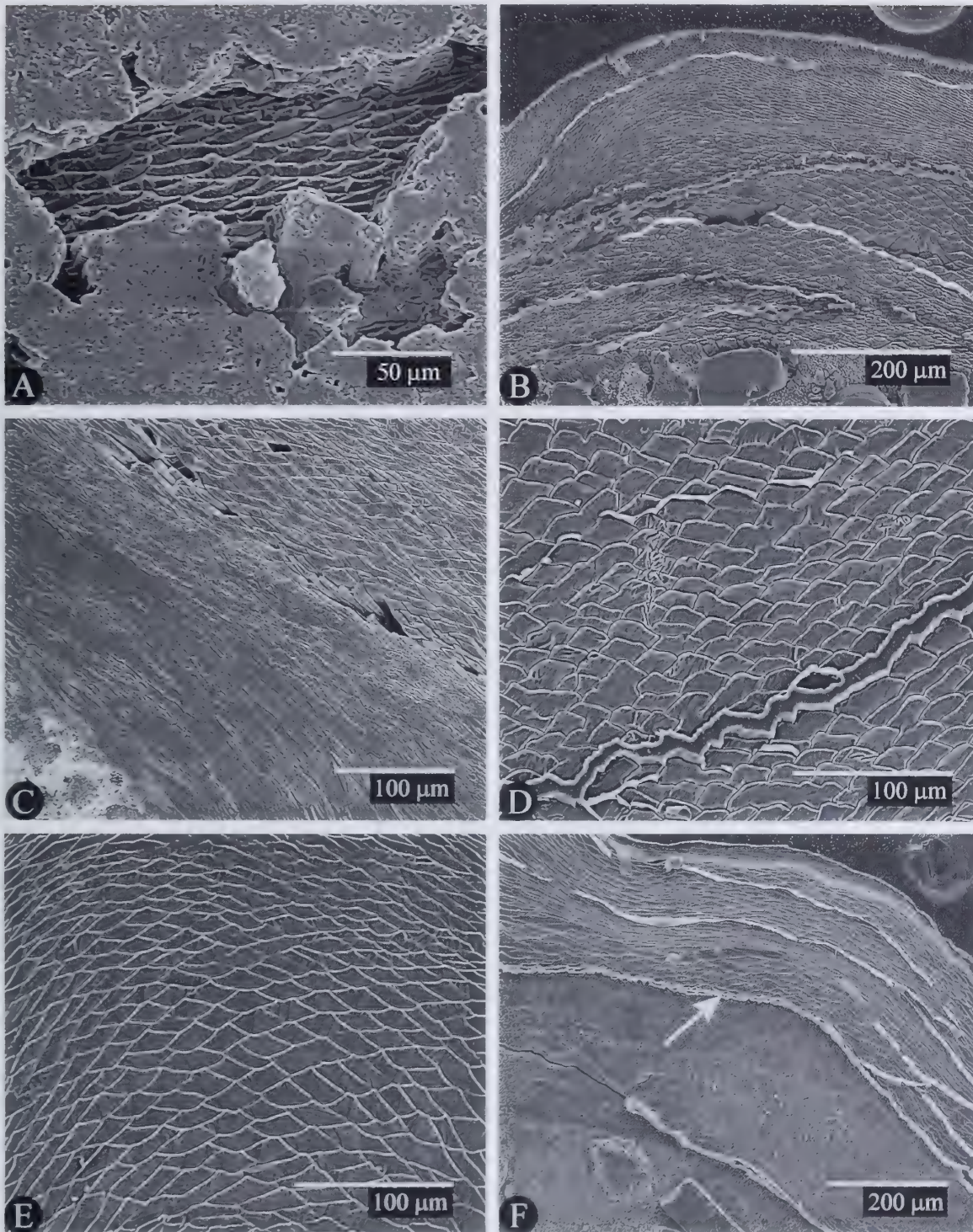
*Cretirhynchia minor* Pettitt, Upper Turonian (Nekvasilova, 1974) was recently removed from the genus *Cretirhynchia* (Simon and Owen, 2001). The shell of this minute





**Figure 3.** **A.** *Cretirhynchia* sp. 2, Nikopol, Lower Maastrichtian, Bulgaria, sample 45-10. Sulcus - section through the whole shell thickness, external surface below. Primary layer missing. Sublayer of finer anisometric fibres in the outermost part of the shell. **B.** *Cretirhynchia exsculpta* Pettitt, Brighton, E. Sussex, England, Lower Campanian, *Marsupites* Zone, sample 7a. Whole shell thickness. Primary layer below. **C.** *Cretirhynchia exsculpta* Pettitt, Brighton, E. Sussex, England, Lower Campanian, *Marsupites* Zone, sample 7b. Section through the rib. Primary layer above. **D.** *Cretirhynchia* aff. *cuneiformis* Pettitt, Čížkovice near Lovosice, Czech Republic, Upper Turonian, sample 19. Whole shell thickness, primary layer above. **E, F.** *Cretirhynchia minor* Pettitt, Čížkovice near Lovosice, Czech Republic, Upper Turonian, sample 22b. **E** - Section through a rib. **F** - Boundary between the primary and the secondary layers, anvil-like fibres.





**Figure 4.** **A.** *Cretirhynchia bohémica* (Schloenbach), Malnice near Louny, Czech Republic, Lower Turonian, sample 20b. Small fragment of non silicified fibres (low relief), strong silicification (high relief). **B.** *Septatoechia inflata* Titova, Tuarkir, Turkmenistan, Upper Maastrichtian, sample 26b. Section through a rib, primary layer missing, secondary differentiated. High relief silicified organic sheets subparallel to the shell surface separate the bundles of fibres with different orientation. **C.** *Septatoechia inflata* Titova, Novachene, Bulgaria, Upper Maastrichtian, sample 52a. Boundary between the secondary fibres (upper right corner) and a very thick myotest (lower left half) in the ventral valve. **D.** *Septatoechia amudariensis* (Katz), Nardylvaldivy, Badkhyz region, East Turkmenistan, Upper Maastrichtian, sample 27a. Secondary fibres crossed by two subparallel bands of high relief silicified organic sheets. **E.** *Septatoechia* aff. *Rhynchonella baugasii* d'Orbigny, Komunari, Bulgaria, Upper Campanian, sample 51b. Orthodoxly stacked fibres in a rib. **F.** *Belbekella mutabilis* Lobatscheva, Kuibyshevo, SW Crimea, Russia, Berriassian, sample 32b. Section through the whole shell. Myotest occupying the interior half of the shell thickness separated by a silicified organic sheet (arrow).



rhynchonellide is 450  $\mu\text{m}$  thick. The primary layer is microgranular, partly recrystallized (Figure 3F) and 20–25  $\mu\text{m}$  thick. Close to the exterior, at about one third of the shell thickness, finer anisometric fibres are developed;  $W=30\text{--}45\text{ }\mu\text{m}$ ;  $T=6\text{--}10\text{ }\mu\text{m}$ ;  $C_2=3.5\text{--}6.5$ . The remaining part of the shell is built up of uniformly arranged more isometric fibres, ( $W=25\text{--}40\text{ }\mu\text{m}$ ;  $T=10\text{--}17\text{ }\mu\text{m}$ ;  $C_1=2.2\text{--}3.5$ ); (Figure 3E).

*Cretirhynchia bohemia* (Schloenbach), Lower Turonian (Nekvasilova, 1974) was strongly silicified and only some isolated fragments of the original structure were preserved. The shell is relatively thick – 480  $\mu\text{m}$  and the primary layer is recrystallized, 30–40  $\mu\text{m}$  thick. Judging from the narrow spots of non-altered secondary shell (Figure 4A), the fibres are anisometric, very fine and anvil-like ( $W=16\text{--}40\text{ }\mu\text{m}$ ;  $T=4\text{--}8\text{ }\mu\text{m}$ ;  $C=3.2\text{--}7$ ). These are amongst the most anisometric fibres of all the studied species, referable to *Cretirhynchia*, and are very similar to the fibres in *Cyclothyris*. As Nekvasilova (1974) suggested, the generic assignment of this species is uncertain and new data are necessary to elucidate in detail its affinities.

#### **Septatoechia Lobatscheva and Titova, 1977**

The type species *Septatoechia inflata* Titova was investigated using representatives from the type locality in Turkmenistan, Lower Maastrichtian (Figure 4B) (Lobatscheva and Titova, 1977) and from Bulgaria, Upper Maastrichtian (Figure 4C) (Motchurova-Dekova, 1996). In addition, two other species were studied: *Septatoechia amudariensis* (Katz) from the Upper Maastrichtian in Turkmenistan (Figure 4D) (Lobatscheva and Titova, 1977) and from Bulgaria, and *Septatoechia* aff. *Rhynchonella baugassii* d'Orbigny, Upper Campanian from Bulgaria (Figure 4E) (Motchurova-Dekova, 1996). This genus is characterized internally by a very high median septum and subparallel to convergent dental plates. The shell is very thick, reaching 1000–2000  $\mu\text{m}$ . The primary layer is relatively thin: 30–50  $\mu\text{m}$ . The secondary layer is composed of many packages of differently orientated relatively isometric fibres. They are 15–40  $\mu\text{m}$  wide and 8–30  $\mu\text{m}$  thick.  $C_1$  starts from very low values ( $C_1=0.8\text{--}3$ ). Externally and internally thinner anisometric fibres are developed. Centrally, the shell is built up of relatively isometric thicker fibres. The main part of the fibres is rhombic, or less commonly anvil-like, especially the thinner fibres. Before erecting the genus *Septatoechia* (Lobatscheva and Titova, 1977), its representatives were assigned to the genera *Cyclothyris* or *Cretirhynchia* because of internal and external similarities. In fact *Septatoechia* represents an interesting mixture of morphologic characteristics, typical of *Cyclothyris* and *Cretirhynchia*. Judging from ultrastructural evidence, *Septatoechia* is much closer to *Cretirhynchia sensu stricto*, displaying a very thick shell, and relatively isometric and similarly sized rhombic fibres in the secondary shell. As in *Cretirhynchia*, the rhombic cross-sections of the fibres in *Septatoechia* have rounded edges. In both genera the myotest is typically very thick (Figure 4C). The fibres in *Septatoechia*, however, are more isometric and the secondary layer seems to be differentiated (Figure 4B).

Single representatives of five other Cretaceous

rhynchonellide genera were studied for comparison.

#### **Belbekella Moisseev, 1939**

The shell thickness in the type species *Belbekella aigulensis* Moisseev, Berriassian (Lobatscheva, 1993) is 600  $\mu\text{m}$ . The primary layer, built up of acicular calcite, is 40–100  $\mu\text{m}$  thick. The fibres are uniformly arranged and anvil-like ( $W=15\text{--}40\text{ }\mu\text{m}$ ;  $T=2\text{--}6\text{ }\mu\text{m}$ ;  $C_1=4\text{--}7$ ). A more posterior cross-section, cutting the muscle field of the pedicle valve of *Belbekella mutabilis* Lobatscheva, Berriassian (Lobatscheva, 1993) was studied. A very thick myotest (up to 300  $\mu\text{m}$ ) was observed (Figure 4F).

#### **Lamellaerhynchia Burri, 1953**

*Lamellaerhynchia geokderensis* Moisseev, Upper Barremian, Turkmenistan (Coll. Lobatscheva) shows shell thickness of 700–1000  $\mu\text{m}$ . The primary layer is microgranular and 20–25  $\mu\text{m}$  thick. The secondary layer is built up of fibres, more anisometric and finer ones close to the exterior shell surface ( $W=10\text{--}20\text{ }\mu\text{m}$ ;  $T=3\text{--}5\text{ }\mu\text{m}$ ;  $C_2=3\text{--}5$ ) and more isometric and larger ones toward the interior margin of the shell ( $W=25\text{--}30\text{ }\mu\text{m}$ ;  $T=8\text{--}15\text{ }\mu\text{m}$ ;  $C_1=2\text{--}3$ ). The majority of the fibres have anvil-like cross-sections, but some of the larger and thicker fibres tend to have rhombic sections (Figure 5A).

#### **Burrirhynchia Owen, 1962**

The type species *Burrirhynchia leightonensis* Walker, Lower Albian (Owen, 1956) has a shell thickness of 500–600  $\mu\text{m}$ . The primary layer is 20 to 50  $\mu\text{m}$  thick. The secondary layer is composed of uniformly arranged anisometric anvil-like fibers (Figure 5D);  $W=20\text{--}50\text{ }\mu\text{m}$ ;  $T=5\text{--}10\text{ }\mu\text{m}$ ;  $C_1=3.5\text{--}6$ , with average values of  $C_1$  around 5. Thinner fibres are developed close to the outer surface (Figure 5D), but there is no noticeable differentiation of the secondary layer (Figures 2D, 5C).

#### **Almerarhynchia Calzada, 1974**

*Almerarhynchia pocoviana* Calzada and Pocovi (1980), Upper Campanian has a relatively thin shell – 290  $\mu\text{m}$ . The primary layer is 20  $\mu\text{m}$  thick and strongly recrystallized. The secondary layer is built up of monotonously stacked rhombic and parallelogram, to rarely anvil-like fibres, with predominance of anisometric rhombic fibres. Although the majority of fibres ( $W=25\text{--}35\text{ }\mu\text{m}$ ;  $T=4\text{--}10\text{ }\mu\text{m}$ ;  $C_1=3\text{--}7$ ) are anvil-like in cross sections (Figure 5E), they are not convex as in other species but tend to be rhombic. Close to the primary layer finer fibres are developed ( $W=15\text{--}20\text{ }\mu\text{m}$ ;  $T=3\text{--}6\text{ }\mu\text{m}$ ;  $C_2=3\text{--}6$ ). Similar finer fibres, but not well differentiated, are developed close to the internal part of the shell. The finer fibres do not constitute a distinct sublayer. The overall appearance of the cross section of the secondary layer is uniform.

#### **Grasirhynchia Owen, 1968**

The shell thickness of the type species *Grasirhynchia grasiiana* (d'Orbigny), Cenomanian, (Owen, 1968) is 300  $\mu\text{m}$ .

The primary layer is 15–20  $\mu\text{m}$  thick. The shape of the fibres in the secondary layer is blurred by the strong silicification of the interfibre spaces, vacated after the early



**Table 1.** Comparative ultrastructural characteristics of four Cretaceous rhynchonellide brachiopod genera.

Genus	Fibre dimensions			Peculiarities of the shell ultrastructure
	W ( $\mu\text{m}$ )	T ( $\mu\text{m}$ )	C=W/T	
<i>Orbirhynchia</i>	35–120	10–50	1–4	rhombic or parallelogramic, relatively more isometric fibres, uniformly arranged.
<i>Cyclothyris</i>	15–30	2–10	4–8	anvil-like anisometric fibres; often differentiated secondary layer.
<i>Cretirhynchia</i> ( <i>C. plicatilis</i> sensu Aliev and Titova, 1988)	20–40	15–25	1.2–2.5	thick shell, rhombic, rarely anvil-like, relatively isometric fibres.
<i>Septatoechia</i>	15–40	8–30	0.8–3	very thick shell; rhombic, rarely anvil-like, relatively isometric fibres; often differentiated secondary layer.

diagenetic decay of the organic sheaths (Figure 5F). The silicification is stronger in the umbonal part of the shell. In this case it is probable that the shape and dimensions of the fibres were altered by the diagenesis. The secondary layer is built up of two kinds of uniformly distributed fibres: (1) finer close to the exterior ( $W = 15\text{--}25\ \mu\text{m}$ ;  $T = 2\text{--}5\ \mu\text{m}$ ;  $C_2 = 4.5\text{--}9$ ) and (2) larger in the central and internal part of the shell ( $W = 35\text{--}55\ \mu\text{m}$ ;  $T = 8\text{--}12\ \mu\text{m}$ ;  $C_1 = 3\text{--}4.5$ ). The transition from the finer to the larger fibres is continuous. The majority of the fibres are rhomboidal. Some of them, especially close to the primary layer, show anvil-like sections.

### Conclusions

This study generally confirms the validity of the classification of Kamyshan (1977) who distinguished two types of fibrous structures of the secondary layer among Mesozoic rhynchonellides: **coarse-fibrous basiliolidine type** and **fine fibrous rhynchonellidine type**. The studied Cretaceous genera have been accommodated in this scheme, although large variation in fibre size is noticed. Data about fibre shape and size of genera, for which sufficient material was available, are given in Table 1.

Along with the previously studied genera *Erymnaria* and *Costerymnaria* (Motchurova-Dekova and Taddei Ruggiero, 2000), the genus *Orbirhynchia* is characterized by a coarse fibrous basiliolidine type microstructure of the secondary layer. *Orbirhynchia* has large fibres with well-defined rhombic cross-sections. It seems that during the Cretaceous the representatives of the pugnacoid stock (Manceñido and Owen, 1996, 2000) developed a coarse fibrous secondary layer.

All the remaining genera can be accommodated within the group of species with a **fine fibrous rhynchonellidine type** of ultrastructure, although they display a larger fibre size than those reported for the Jurassic and Lower Cretaceous representatives (Smirnova, 1984). When compared to the Upper Cretaceous *Orbirhynchia*, however, all the other studied genera are characterized by a smaller fibre size (Table 1).

*Cyclothyris* is characterized by a typical rhynchonellidine type ultrastructure sensu Kamyshan (1977).

*Cretirhynchia* and *Septatoechia* are also classified within the rhynchonellidine group. Both genera, however, have

somewhat larger fibres than *Cyclothyris*, and with a peculiar relatively isometric shape in cross-section. It is suggested that *Cretirhynchia* and *Septatoechia* are more closely related to each other than to any of the other studied genera. Additional investigations on other representatives of *Cretirhynchia* are necessary to confirm this relationship.

*Belbekella*, *Lamellaerhynchia*, *Almerarhynchia*, *Burrirhynchia* and *Grasirhynchia* have anisometric fibres, similar to those of *Cyclothyris*. Their larger fibre size and undifferentiated secondary layers distinguish them from *Cyclothyris*.

*Burrirhynchia* has uniformly arranged anisometric fibres quite distinct from the pattern of *Cretirhynchia plicatilis* sensu Aliev and Titova, 1988. *Burrirhynchia* seems closer to *Cyclothyris* judging by similarities in the fibre shape. The fibre size in *Burrirhynchia* shells, however, is larger. Before drawing conclusion about the relationship between *Burrirhynchia* and *Cretirhynchia* suggested by Owen (1962), the shell ultrastructure of the type species *Cretirhynchia plicatilis* should also be studied.

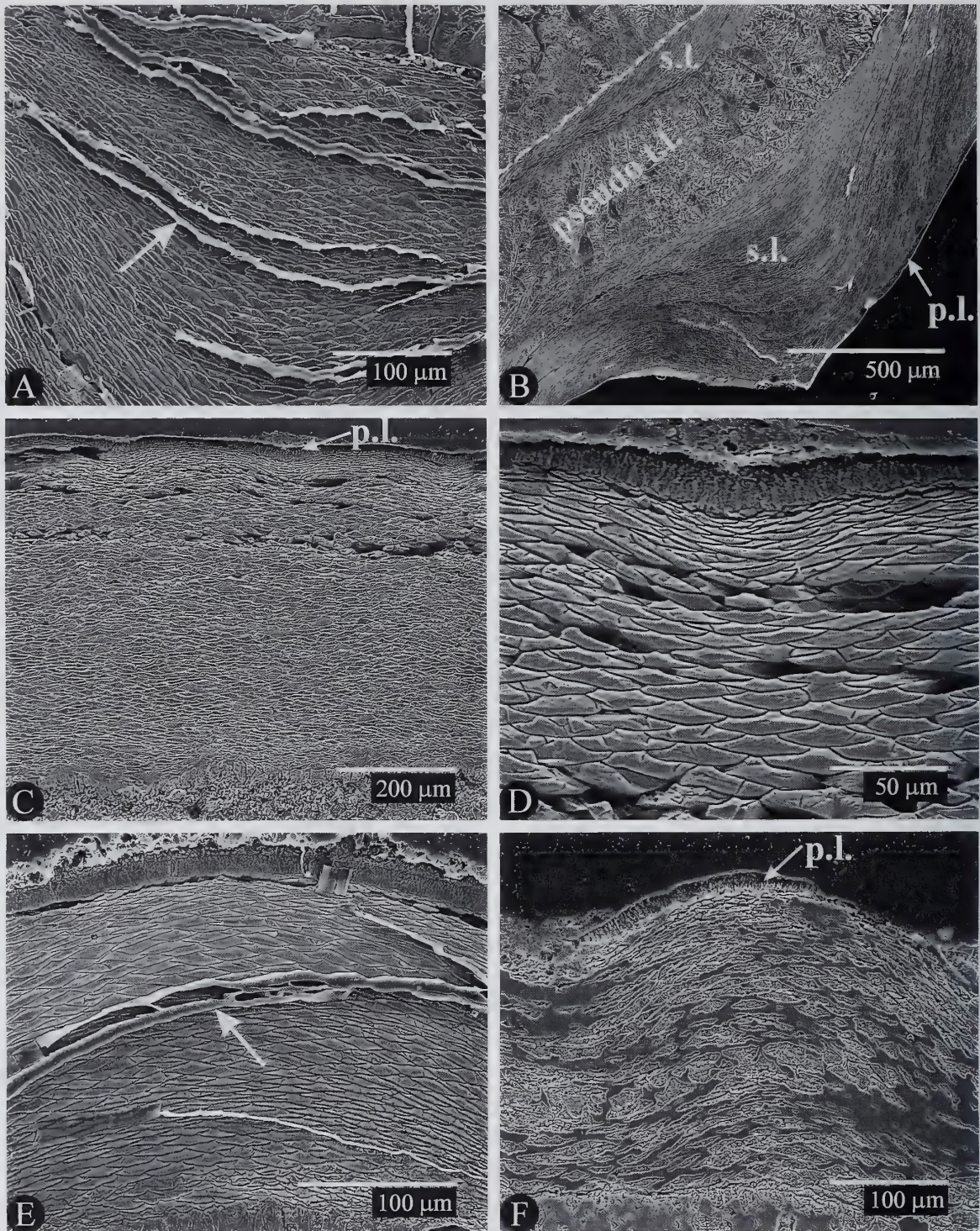
In summary it appears that the genera belonging to the Cretaceous representatives of the hemithiridoid and rhynchonelloid stocks (Manceñido and Owen, 1996, 2000) display a fine fibrous rhynchonellidine type microstructure of the secondary layer.

Finally it should be pointed out that the benefits of using shell microstructural data for the purposes of distinguishing taxa should not be overestimated. Sometimes the dimensions of the fibres and the texture of the secondary layer were found to vary widely from one section to another, even in one specimen. A complete pattern of the shell ultrastructure can be obtained only if a set of sections, both transverse and longitudinal, is made and examined and if sufficient numbers of species from each genus are studied.

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**Figure 5.** **A, B.** *Lamellaerhynchia geokderensis* (Moisseev in Weber) from Keldje, Tuarkyr, Turkmenistan, Upper Barremian. **A** – sample 30a, rib, internal shell surface on the top. Secondary shell, subparallel silicified organic sheets crossing the shell (arrow). **B** – sample 30b, rib. Primary layer (p.l.) partly preserved. A pseudo-tertiary (diagenetic) layer (pseudo t.l.) of calcite prisms is developed in the interior of the secondary layer (s.l.). The dashed white line indicates the internal surface of the shell overgrown by diagenetic calcite prisms in the upper left corner. **C, D.** *Burrirhynchia leightonensis* (Walker), Leighton Buzzard, Bedfordshire, England, Lower Albian, *L. regularis* subzone, **C** – sample 4b. The whole shell thickness, primary layer (p.l.) above. **D** – close up of the area arrowed in **C**. **E.** *Almerarhynchia pocoviana* Calzada and Pocovi, Sierra de Mont-Roig, Spain, Upper Campanian, sample 25a. The whole shell thickness, primary layer above, recrystallized. Silicified organic sheets crossing the section (arrow). **F.** *Grasiirhynchia grasiiana* (d'Orbigny) from Warminster, Wiltshire, England, Lower Chalk, Cenomanian, sample 9b. Section through a rib, strongly silicified and recrystallized secondary shell; partly preserved primary layer (p.l.) above.



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- ◎第151回例会は、2002年1月26日（土）、1月27日（日）の両日にわたり鹿児島大学理学部で開催されます。1月27日（日）午後に公開講演として「21世紀は自然史の時代 ―古生物学・フィールド科学からの提言―：世話人、森 啓・矢島道子；平成13年度科研費研究成果公开发表（B）」を実施致します。また1月26日（土）には、昨年と今年度の学術賞受賞者の特別講演5件を予定しております。一般講演の申し込み締切は2001年11月30日（金）です。
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## CONTENTS

- Tatsuro Matsumoto and Takemi Takahashi:** A study of *Hypoturrillites* (Ammonoidea) from Hokkaido (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-XCI) ..... 229
- Tatsuhiko Yamaguchi and Hiroki Hayashi:** Late Miocene ostracodes from the Kubota Formation, Higashi-Tanagura Group, Northeast Japan, and their implications for bottom environments ..... 241
- Hiroaki Karasawa and Hisayoshi Kato:** The systematic status of the genus *Miosesarma* Karasawa, 1989 with a phylogenetic analysis within the family Grapsidae and a review of fossil records (Crustacea: Decapoda: Brachyura) ..... 259
- Kazuyoshi Moriya, Hiroshi Nishi and Kazushige Tanabe:** Age calibration of megafossil biochronology based on Early Campanian planktonic foraminifera from Hokkaido, Japan ..... 277
- Jun-ichi Tazawa:** Middle Permian brachiopods from the Moribu area, Hida Gaien Belt, central Japan .... 283
- Kazushige Tanabe, Royal H. Mapes and David L. Kidder:** A phosphatized cephalopod mouthpart from the Upper Pennsylvanian of Oklahoma, U. S. A. .... 311
- Neda Motchurova-Dekova:** Taxonomic and phylogenetic aspects of the shell ultrastructure of nine Cretaceous rhynchonellide brachiopod genera ..... 319



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# Middle Miocene ostracods from the Fujina Formation, Shimane Prefecture, Southwest Japan and their paleoenvironmental significance

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**Abstract.** Thirty-five ostracod species belonging to 18 genera are recognized from the Middle Miocene Fujina Formation (ca. 14–12 Ma), 3 km southwest of Matsue City, Shimane Prefecture, Japan. Most of these species are part of the recent Japan Sea proper water fauna; they are also classified into 4 categories, circum-polar, cryophilic, endemic cool-temperate and temperate species. These ostracod assemblages indicate that the Fujina Formation was deposited under a cold-water environment. Ten new species, *Ambtonia shimanensis*, *A. takayasui*, *Acanthocythereis fujinaensis*, *A. izumoensis*, *Cluthia tamayuensis*, *C. subjaponica*, *Kotoracythere tsukagoshii*, *Laperousecythere ikeyai*, *Palmoconcha irizukii*, and *Robertsonites yatsukanus* are described.

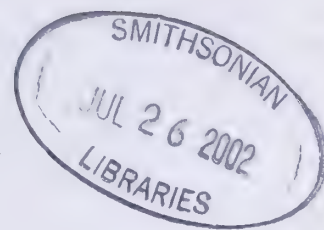
**Key words:** Fujina Formation, Japan Sea proper water, Middle Miocene, ostracods, paleoenvironment

## Introduction

The Japan Sea developed as a result of back-arc spreading prior to 16 Ma and then further expanded by clockwise rotation of the southwestern part of the Japanese islands beginning 15 Ma (Otofuji and Matsuda, 1984). During this short period (ca. 16.5–15 Ma), a tropical to subtropical molluscan fauna, called the Kadonosawa Fauna, spread widely around the Japanese islands. At about 15 Ma, this Kadonosawa fauna was replaced by a cool to temperate molluscan fauna, the Shiobara-Yama type fauna in the Japan Sea region (Chinzei, 1986). According to Chinzei (1986), this drastic faunal change in molluscs was caused by the closure of the Tsushima Straits in the western portion of the Japan Sea. Based on studies of molluscan assemblages in the Middle Miocene of the San'in district along the Japan Sea, the shallow embayment facies (the Shiobara Fauna) appeared after the Omori period (ca. 14.5–15 Ma). During the Fujina period (ca. 14–12 Ma), the molluscan assemblages were accompanied by an off-shore facies (the Yama Fauna) and an increase in colder species of the Shiobara Fauna (Takayasu *et al.*, 1992).

Thus, it is thought that the Fujina Formation was deposited under a cold-water environment which resulted from the closure of the Tsushima Straits. However, the presence of warm-water cephalopod species (*Aturia* sp. and *Argonauta tokunagai*) in several horizons may suggest the influence of a warm-water current (Sakumoto *et al.*, 1996).

Because benthic ostracods do not have a pelagic life stage, they can be easily isolated by environmental barriers. Although Miocene ostracod assemblages in Japan have been reported from several localities (Ishizaki, 1963, 1966; Yajima, 1988, 1992; Irizuki, 1994; Irizuki and Matsubara, 1994, 1995; Ishizaki *et al.*, 1996; Irizuki *et al.*, 1998), the one report from the marine sediments in the southwest of Japan only covered the early Middle Miocene Bihoku Group (Yajima, 1988). To describe the ostracod assemblages in the Fujina Formation, therefore, it is very important to consider marine paleoenvironments of the Japan Sea coast and to examine their paleoenvironmental significance.



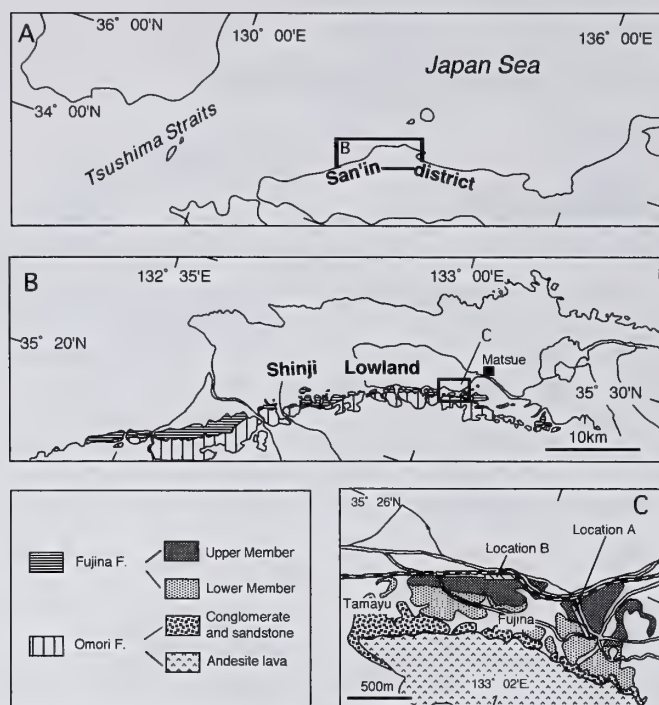


Figure 1. Map of the study area.

### Geological setting of Fujina Formation

The Fujina Formation was named by Tomita and Sakai (1937), then redefined by Ogasawara and Nomura (1980) and Takayasu and Nakamura (1984). This formation covers over 50 km, striking approximately EW to NE-SW and dipping about 10°N along the southern part of the Shinji Lowland (Figure 1). It is about 500 m in maximum thickness and conformably overlies the Omori Formation, which is composed of andesite lava in the lower part and shallow marine andesitic conglomerate and sandstone in the upper part (Kano *et al.*, 1994). The Fujina Formation near the type locality (this study area) is divided into the Lower and Upper Members by lithology. The Lower Member is composed of alternating layers of massive, gray, very fine-grained sandstone (0.5–5 m in thickness) containing calcareous nodules, and massive, dark gray siltstone (0.5–1 m in thickness). The sediments of the uppermost part of this member are made of a medium-grained sandstone (0.5 m in thickness) containing pebbles. The Upper Member is mainly composed of a massive, dark gray siltstone which is intercalated with felsic tuff layers (2 m in thickness), calcareous nodule beds, and “*Modiolus*” beds (0.3 m in thickness) in the uppermost part. Many marine molluscs, vertebrates (e.g., *Desmostylus japonicus* and *Carcharodon megalodon*) and decapods occur in all of the Fujina Formation (Kano *et al.*, 1994). Based on the planktonic

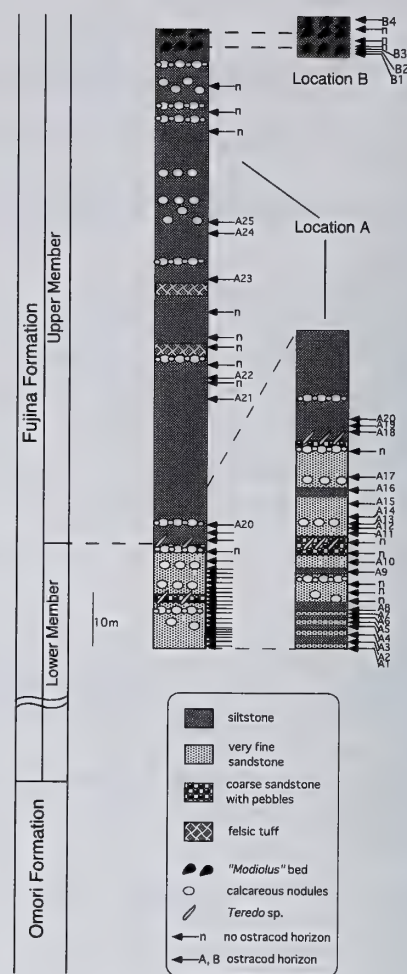


Figure 2. Columnar sections of the Fujina Formation.

foraminifers, the Upper Member of the Fujina Formation is assigned to N.10–11 of Blow's zones (14.6/14.8–12.4 Ma) (Nomura and Maiya, 1984).

### Materials and methods

Fossiliferous sediment samples used in this study were collected from the upper part of the Lower Member to the Upper Member of the Fujina Formation at two locations (Figure 2). Each of the dried sediment samples (80 g) of a total of 46 collected were disaggregated, making use of naphtha for rock maceration (Maiya and Inoue, 1973), washing through a 235 mesh (63  $\mu$ m) sieve, and drying again. This procedure was repeated until the whole sediment sample was disintegrated. A fraction coarser than 120 mesh (125  $\mu$ m) sieve was sieved and all the ostracod specimens present were picked.



	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12	A13	A14	A15	A16	A17	A18	A19	A20	A21	A22	A23	A24	A25	B1	B2	B3	B4
<i>Ambtonia shimanensis</i> sp. nov.											4				4	8		1		7									
++ <i>Ambtonia takayasui</i> sp. nov.							2				2								4										
- <i>Acanthocythereis dunelmensis</i> (Norman, 1865)																						2	6	1	1	13	1	9	15
<i>Acanthocythereis fujinaensis</i> sp. nov.								1			4		5																
<i>Acanthocythereis izumoensis</i> sp. nov.											5			8	10	8			2										
++ <i>Acanthocythereis koreana</i> Huh and Whatley, 1997	11							1		2	38	2	2	16	57	29	31	39	11	30									
- <i>Acanthocythereis tsurugasakensis</i> Tabuki, 1986																										8	5		1
<i>Acanthocythereis</i> sp.1											2										2								
<i>Acanthocythereis</i> sp.2																					4						2		
+ <i>Calistocythere japonica uranipponica</i> Hanai, 1957																	1												
+ <i>Calistocythere kyongjuensis</i> Huh & Whatley, 1997																2													
<i>Cluthia subjaponica</i> sp. nov.											1							3		1									
<i>Cluthia tamayuensis</i> sp. nov.	3						1									2	7		1	1									
<i>Cluthia</i> sp.																										3			
<i>Cytheropteron</i> sp.																11											2		
++ <i>Falsobuntonia taiwanica</i> Malz, 1982																			2		2								
<i>Kotoracythere tatsunokuchensis</i> Ishizaki, 1966											1																		
++ <i>Kotoracythere tsukagoshi</i> sp. nov.	44		1	2	6	5	8	13		6	4			2	5	37	13	11	9	3	15								
<i>Kinthe</i> sp.1																				1									
<i>Kinthe</i> sp.2																2	1		2										1
<i>Laperousecythere ikeyai</i> sp. nov.					2						23	9	5	7	26	1	3	3	11										
<i>Laperousecythere</i> sp.																													3
<i>Loxococoncha subkotoriforma</i> Ishizaki, 1966	1																												
<i>Loxococonchidea</i> sp.							1			2									2										
- <i>Munseyella hatatensis</i> Ishizaki, 1966																													1
++ <i>Paijienborchella</i> cf. <i>tsurugasakensis</i> Tabuki, 1986	62			1					1	1	20		2		21	14	31	39	3	19						4	5	5	7
- <i>Palmenella limicola</i> (Norman, 1865)	1						1				1			2	3	1	1	2	1										
++ <i>Palmococoncha irizuki</i> sp. nov.	2										8			1	39	31	31	33	6	52						1			
<i>Robertsonites japonicus</i> (Ishizaki, 1966)	7	1			2			2		6							2												
- <i>Robertsonites reticuliformis</i> (Ishizaki, 1966)								3		3				2	12		7	1	7	3	1								
- <i>Robertsonites</i> cf. <i>tuberculatus</i> (Sars, 1866)																													2
<i>Robertsonites yatsukanus</i> sp. nov.																							1			18	1	5	
<i>Robertsonites</i> sp.																							1				3		1
<i>Semicytherura</i> sp.																		1											
<i>Urocythereis pohangensis</i> Huh and Whatley, 1997	29										10	5	6	11	22	9	5	8	7	5		3							
No. of specimens	160	1	1	2	11	5	12	21	1	9	134	16	22	52	248	125	121	146	55	141	1	2	11	1	1	49	15	22	30
No. of species	9	1	1	1	4	1	4	5	1	3	16	3	6	8	14	14	9	15	10	12	1	1	4	1	1	7	5	5	7
Weight of Sediments (g)	1520	80	80	80	960	880	1440	1680	80	800	1120	320	320	1040	1680	1440	1440	1120	1040	1040	80	80	240	80	80	2240	1440	1680	1760

Figure 3. List of ostracod species from the Fujina Formation (—: circumpolar species; -: cryophilic species; +: endemic cool-temperate species; ++: temperate species).

### Characteristic ostracods from Fujina Formation

Thirty-five species in 18 genera of ostracods were identified from 29 samples (25 samples from Location A and 4 samples from Location B); (Figure 3). Ostracods from the Fujina Formation can be divided into four different temperature-related categories: 1) circumpolar, 2) cryophilic, 3) endemic cool-temperate and 4) temperate species. Cronin and Ikeya (1987) recognized 26 circumpolar and 21 cryophilic species from several Plio-Pleistocene formations of Japan. They referred to ostracods known from Recent and/or Cenozoic deposits of the North Atlantic and adjacent arctic seas as "circumpolar species", and species that typically occur with circumpolar species in Japanese deposits (in most cases being members of high-latitude genera) as "cryophilic species". Irizuki (1994) selected 13 circumpolar, 9 cryophilic and 4 endemic cold-water species from the Late Miocene Fujikotogawa Formation, Akita Prefecture, northern Japan. Irizuki and Matsubara (1995) described 5 circumpolar and 8 cryophilic species from the early Middle Miocene Suenomatsuyama Formation, Iwate Prefecture, northeastern Japan. They pointed out that

circumpolar and cryophilic species preferred living in colder water than other species even during the Miocene. They also recognized 13 temperate species that preferred warmer waters than those mentioned as circumpolar and cryophilic indicators. The following 4 categories concern their (paleo) biogeographic distributions in the northern hemisphere and the relative water temperatures during deposition of the Fujina Formation.

#### 1. Circumpolar species (4 species)

These species were widely distributed from middle- to high-latitude regions in the Miocene (Figure 4; regions 1–10), and dominate the upper horizons of the Fujina Formation. *Acanthocythereis dunelmensis* (Norman), *Munseyella hatatensis* Ishizaki, *Palmenella limicola* (Norman) and *Robertsonites tuberculatus* (Sars).

#### 2. Cryophilic species (2 species)

Since the Miocene, these species have been distributed around the Japanese islands (Figure 4; regions 5 and 9), and are prominent in the upper horizons of the Fujina Formation with the circumpolar species. *Acanthocythereis tsurugasakensis* Tabuki and *Robertsonites reticuliformis*



**Figure 4.** Geographic and stratigraphic distributions of characteristic species of the Fujina Formation. **R** [2a–e: Barents Sea (a–e: Elofson, 1941; b: Hartmann, 1992, 1993; c: Freiwald and Mostafawi, 1998); 2f: Russian Harbour (Neale and Howe, 1975); 3a, b: Greenland Sea (Elofson, 1941); 3c: Baffin Bay (Elofson, 1941); 3d: Labrador Sea (Hulings, 1967); 6a: North Sea (Elofson, 1941; McKenzie *et al.*, 1989); 6b: Baltic Sea (Elofson, 1941; Rosenfeld, 1977); 7a: England (Elofson, 1941); 7b: Ireland (Elofson, 1941); 7c: Labrador Sea (Hulings, 1967); 7d: Bay of Biscay (Caralp *et al.*, 1967; Caralp *et al.*, 1968); 8: Gulf of Alaska (Brouwers, 1988, 1990); 9a: Sendai Bay (Ikeya and Itoh, 1991); 9b: off Shimane (Ikeya and Suzuki, 1992); 9c: Ulleung Basin (Cheong *et al.*, 1986); 9d: Fukuoka (Hanai, 1957a)]. **H** [3a–c: Baffin Bay (Neale and Howe, 1975); 3d–f Baffin Island (Neale and Howe, 1975); 6: Sandnes Clay (Lord, 1980); 7a: Labrador Sea (Neale and Howe, 1975); 7b, c: off Nova Scotia (Neale and Howe, 1975); 9: Takahama shell bed (Kamiya and Nakagawa, 1993); 10: off New York (Neale and Howe, 1975)]. **Q** [4a: Prudhoe Bay Boreholes (McDougall, Brouwers and Smith, 1986); 4b, c: Gubik F. (Swain, 1961, 1963); 5a: Wakimoto F. (Cronin and Ikeya, 1987); 5b: Sasaoka F. (Cronin and Ikeya, 1987); 6: Esbjerg deposit (Bassiouni, 1965); 7a: Tyrrel Sea F. (Cronin, 1989); 7b, c: East Goldthwait Sea F. (Cronin, 1989); 7d, e: St. Lawrence Lowland (Cronin, 1981); 9: Shimosa G. (Yajima, 1982; Yajima and Lord, 1990; Ozawa *et al.*, 1995); 10: off New York (Neale and Howe, 1975)]. **P** [3: Tjornes Beds (Cronin, 1991); 5a: Setana F. (Cronin and Ikeya, 1987); 5b: Tomikawa F. (Cronin and Ikeya, 1987); 5c: Daishaka F. (Tabuki, 1986); 9a: Kitaura F. (Cronin and Ikeya, 1987); 9b: Sawane F. (Cronin and Ikeya, 1987); 9c: Junicho F. (Cronin and Ikeya, 1987); 9d: Omma F. (Cronin and Ikeya, 1987; Kamiya *et al.*, 1996); 9e: Ssukou F. (Malz, 1982)]. **N** [1: Kap Kobenhavn F. (Brouwers *et al.*, 1991; Penney, 1993); 3: Lodin Elv F. (Penney, 1993); 9a: Tatsunokuchi F. (Ishizaki, 1966); 9b: Tentokuji F. (Irizuki, 1996)]. **M** [5a: Kadonosawa F. (Irizuki and Matsubara, 1994); 5b: Kamikoani F. (Yajima, 1988); 9a: Hatatate F. (Ishizaki, 1966); 9b: Fujikotogawa F. (Irizuki, 1994); 9c: Togi Mud F. (Yajima, 1988); 9d: Yeonil G. (Huh and Paik, 1992a,b; Huh and Whatley, 1997); 9e: Fujina F. (This study); 9f: Kobana F. (Irizuki *et al.*, 1998); 9g: Shukunohora Sandstone (Yajima, 1988)].

(Ishizaki).

### 3. Endemic cool-temperate species (3 species)

These species are mainly distributed around the Japan Sea area from the Miocene to the Recent (Figure 4; regions 5 and 9), and occur throughout the Fujina Formation. *Callistocythere japonica uranipponica* Hanai, *C. kyongjuensis* Huh and Whatley and *Paijenborchella cf. tsurugasakensis* Tabuki. *C. japonica uranipponica* was recognized by Hanai (1957a) as a subspecies of *C. japonica*, and is restricted along the Japan Sea coast and the Pacific side of northern Japan after the Miocene. *C. kyongjuensis* was reported with some cold-water species in the Early Miocene Chunbuk Conglomerate Formation of Korea (Huh and Paik, 1992a,b). *P. tsurugasakensis* occurs in the Omma Formation (Late Pliocene to Early Pleistocene) with many warm- and a few cold-water species (Ozawa, 1996).

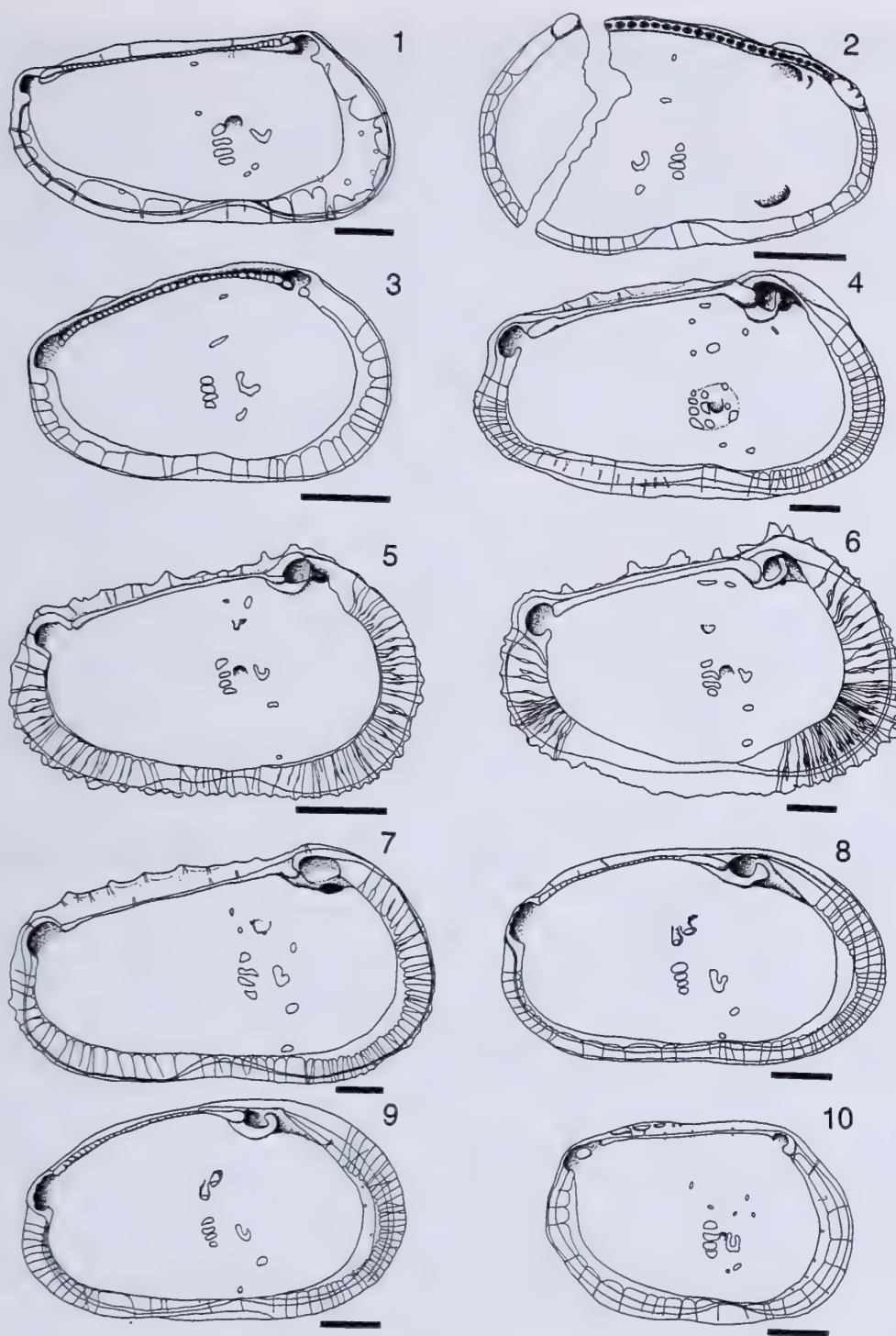
### 4. Temperate species (5 species, including 3 new species)

These have been distributed around the Japanese islands since the Miocene (Figure 4; regions 5 and 9), and dominate into the Lower Member to the lowermost part of the Upper Member of the Fujina Formation. *Acanthocythereis koreana* Huh and Whatley, *A. takayasui* Tanaka sp. nov., *Falsobuntonia taiwanica* Malz and *Kotorocythere tsukagoshii* Tanaka sp. nov. and *Palmoconcha irizukii* Tanaka sp. nov. *A. koreana* was first reported with cold-water species in the Early Miocene Chunbuk Conglomerate Formation of Korea (Huh and Paik, 1992a, b). *A. takayasui* has been reported in the Early Miocene from Mizunami, central Japan with some warm- and shallow-water species (as *F. taiwanica*; Yajima, 1988, pl. 1, fig. 7), but this species occurred with some colder species in the Early Miocene of Korea (as *A. obai*; Huh and Paik, 1992a, pl. 2, fig. 14, and *F. taiwanica*; Huh and Paik, 1992b, pl. 2, fig. 14). *F. taiwanica*, *P. irizukii* and *K. tsukagoshii* occurs in horizons deposited under warm-water conditions of the Early-Middle Miocene Kadonosawa Formation, Iwate Prefecture, northeastern Japan (as *K. sp.*; Irizuki and Matsubara, 1994, pl. 1, fig. 3). *K. tsukagoshii* also occurs in the Omma Formation (Late Pliocene to Early Pleistocene) (as *Pectocythere quadrangulata*; Ozawa, 1996, pl. 8, fig. 2). Thus, it is probable that these temperate species adapted to colder environments during the Miocene in the Japan Sea area.

### Discussion and conclusion

According to Ikeya and Cronin (1993), the Recent Japan Sea proper water is characterized by the ostracod species *A. dunelmensis*, *Elofsonella concinna*, *P. limicola*, *Robertsonites*, *Cluthia* and *Rabilimis*, and these species suggest cold-water isotherms along the upper slope at depths of





**Figure 5.** Internal views of each species. 1: *Kotoracythere tsukagoshii* Tanaka sp. nov., female, LV, paratype, Loc. 1-A15, SUM-CO-1211; 2: *Cluthia tamayuensis* Tanaka sp. nov., female, RV, paratype, Loc. 1-A1, SUM-CO-1217; 3: *Cluthia subjaponica* Tanaka sp. nov., female, LV, paratype, Loc. 1-A15, SUM-CO-1220; 4: *Laperousecythere ikeyai* Tanaka sp. nov., male, LV, paratype, Loc. 1-A11, SUM-CO-1229; 5: *Acanthocythereis fujinaensis* Tanaka sp. nov., female, LV, paratype, Loc. 1-A11, SUM-CO-1234; 6: *Acanthocythereis izumoensis* Tanaka sp. nov., female, LV, paratype, Loc. 1-A17, SUM-CO-1239; 7: *Robertsonites yatsukanus* Tanaka sp. nov., male, LV, paratype, Loc. 2-B1, SUM-CO-1249; 8: *Ambtonia shimanensis* Tanaka sp. nov., LV, paratype, Loc. 1-A19, SUM-CO-1252; 9: *Ambtonia takayasui* Tanaka sp. nov., female, LV, paratype, Loc. 1-A15, SUM-CO-1256; 10: *Palmoconcha irizukii* Tanaka sp. nov., female, LV, paratype, Loc. 1-A15, SUM-CO-1261. Scale bar is 0.10 mm.





100–300 m. These assemblages resemble the Middle Miocene assemblage from the uppermost part of the Lower Member to the Upper Member of the Fujina Formation. Sakumoto *et al.* (1996) reported some cephalopod species that indicate that the paleo-Tsushima warm-water current flowed in the Proto-Japan Sea. Warmer conditions are indicated by the absence of cool-water ostracodes in part of this formation and the presence of prominent circumpolar and cryophilic species towards the upper horizons of the Fujina Formation, so we think that the Fujina Formation gradually became colder and colder towards the upper horizon, and that the warm-water current did not influence the benthic ostracods. Similar results have also been recognized from the benthic molluscan assemblages (Ogasawara and Nomura, 1980; Takayasu, 1986). Hence, it is concluded that during the early Middle Miocene period, temperate Pacific-side species invaded the coastal and offshore seafloor of the Japan Sea, and afterwards, with the change in marine climate and regional tectonic events, some taxa became isolated in embayments and offshore areas and adapted to cooler conditions.

### Systematic descriptions

(by G. Tanaka)

All the illustrated specimens are deposited in the collections of the Shizuoka University Museum (SUM-CO-Number). Type locality of all new species is indicated by the index number: Loc. 1 or 2-horizon number; (Loc. 1: 35° 25.5'N, 133° 02.3'E; Loc. 2: 35° 25.6'N, 133° 01.4'E). Morphological terms follow the usage of Hanai (1961), Scott (1961) and Athersuch *et al.* (1989). The following abbreviations are used in this paper: C, carapace; RV, right valve; LV, left valve; L, length of valve; H, height of valve.

Order Podocopida Sars, 1866

Superfamily Cytheroidea Baird, 1850

Family Eucytheridae Puri, 1954

Subfamily Pectocytherinae Hanai, 1957

Genus *Kotoracythere* Ishizaki, 1966

#### *Kotoracythere tsukagoshii* Tanaka sp. nov.

Figures 5.1, 6.1–6.3

*Kotoracythere* sp. Irizuki and Matsubara, 1994, pl. 1, fig. 3.

*Pectocythere quadangulata* Hanai, Ozawa, 1996, pl. 8, fig. 2.

*Etymology.*—In honor of A. Tsukagoshi (Shizuoka University, Japan) a specialist in ostracod systematics.

*Types.*—Holotype, LV of male, SUM-CO-1208 (L = 0.66 mm, H = 0.32 mm). Paratypes, RV of male, SUM-CO-1209 (L = 0.67 mm, H = 0.32 mm); C of female, SUM-CO-1210 (L = 0.64 mm, H = 0.33 mm); LV of female, SUM-CO-1211 (L = 0.64 mm, H = 0.32 mm).

*Type locality.*—Loc. 1–A15.

*Diagnosis.*—Valve oblong box-shaped. Surface ornamented by scattered deep pits and very weak reticulations. Vestibule widely developed along anteroventral margin. Radial pore canals few. Anterior and posterior teeth of median element composed of upper and lower elements respectively.

*Description.*—Valve oblong box-shaped in lateral view. Anterior margin evenly rounded with infracurvature; dorsal margin straight, sloping gently toward posterior; posterior margin truncated dorsally and rounded ventrally; ventral margin nearly straight. Large sexual dimorphism; in lateral view, male forms more elongate; in dorsal view, female forms having inflated carapace in the posteroventral area. Eye spot not observed. Surface ornamented by scattered deep pits, which are the openings of normal pore canals, and very weak reticulation. In dorsal view, carapace is elongate ovate, widest in the posteromedian area, but compressed in the median area in female forms. In anterior view, carapace subovate, broadest at point near mid-height. Marginal zone broad anteriorly, vestibula widely developed in the anteroventral area and narrowly in the posteroventral area. Marginal pore canals few, 7 in anterior, 5 in posterior. Selvage well developed. Hinge pentodont: In LV, anterior and posterior elements are interiorly opened sockets respectively; median element is a crenulate bar with teeth at anterior and posterior terminations which are composed of upper and lower elements respectively. One V-shaped frontal scar. Four elliptical adductor scars are in a vertical row, the middle two are narrow. Two small elliptical mandibular scars. Two dorsal scars (one elliptical, dorsomedial; one elliptical, mid-dorsal). Prominent fulcral point.

*Remarks.*—This species differs from *K.* sp. widely reported from Plio-Pleistocene formations of north and central Japan (Ishizaki and Matoba, 1985; Tabuki, 1986; Cronin and Ikeya, 1987; Ozawa, 1996), in its very weak reticulation. The present species is distinguished from *Pectocythere tsiuensis* Brouwers, 1990 from the Quaternary

← **Figure 6.** 1–3, *Kotoracythere tsukagoshii* Tanaka sp. nov. 1a–e: male LV, holotype, Loc. 1-A15, SUM-CO-1208; 2a–c: male RV, Loc. 1-A15, SUM-CO-1209; 3a–d: female carapace, Loc. 1-A15, SUM-CO-1210. 4–5, *Cluthia tamayuensis* Tanaka sp. nov. 4a–e: female LV, holotype, Loc. 1-A16, SUM-CO-1215; 5a–c: male RV, paratype, Loc. 1-A15, SUM-CO-1216. 6–7, *Cluthia subjaponica* Tanaka sp. nov. 6a–e: female LV, holotype, Loc. 1-A16, SUM-CO-1218; 7a–c: male LV, paratype, Loc. 1-A15, SUM-CO-1219. 8: *Callistocythere japonica uranipponica* Hanai, 1957, male LV, Loc. 1-A16, SUM-CO-1213. 9: *Callistocythere kyongjuensis* Huh and Whatley, 1997, male LV, Loc. 1-A15, SUM-CO-1214. 10: *Munseyella hatatensis* Ishizaki, 1966, male RV, Loc. 2-B3, SUM-CO-1212. Scale bar is 0.10 mm.

sediments of the Gulf of Alaska, North America, in its very weak reticulation and the outline of the anterior margin.

*Occurrences.*—Early to Middle Miocene and Pleistocene sediments, Honshu, Japan (M5a, M9e and P9d; see Figure 4).

Genus *Munseyella* van den Bold, 1957

*Munseyella hatatensis* Ishizaki, 1966

Figure 6.10

*Munseyella hatatensis* Ishizaki, 1966, p. 153, pl. 19, fig. 2; Cronin and Ikeya, 1987, p. 76, pl. 3, fig. 16; Ikeya and Itoh, 1991, fig. 19A; Huh and Paik, 1992b, pl. 3, fig. 9; Irizuki, 1994, p. 8, pl. 1, fig. 2; Kamiya *et al.*, 1996, pl. 2, fig. 3; Ozawa, 1996, pl. 7, fig. 2.

*Munseyella mananensis* Hazel and Valentine, 1969, p. 749–751, pl. 97, figs. 19–24, pl. 98, figs. 1, 3, 4, 11, 12, text-figs. 4a, b, 5a, e, g; Cronin, 1989, pl. 2, fig. 8.

*Remarks.*—Cronin and Ikeya (1987) thought that *M. hatatensis* was conspecific with *M. mananensis* Hazel and Valentine, 1969. Based on carapace morphology and geographical distribution, I have followed their opinion.

*Occurrences.*—Miocene to Recent sediments of North Atlantic, Japan and Korea (H3a–c, P5a, b, Q5b, Q7a, b, H7a–c, M9a, b, d, e, P9c, d, R9a, Q10, H10; see Figure 4).

Family Leptocytheridae Hanai, 1957

Genus *Callistocythere* Ruggieri, 1953

*Callistocythere japonica uranipponica* Hanai, 1957

Figure 6.8

*Callistocythere japonica uranipponica* Hanai, 1957a, p. 457–459, pl. 9, figs. 3a–c; Ishizaki and Matoba, 1985, pl. 2, fig. 8; Kamiya and Nakagawa, 1993, pl. 2, fig. 1.

*Callistocythere cf. japonica uranipponica* Hanai, 1966, p. 147, pl. 16, fig. 13.

*Remarks.*—*C. japonica uranipponica* was recognized by Hanai (1957a) as a subspecies of *C. japonica*. *C. japonica uranipponica* is distinguished from *C. japonica* in having a more narrowly rounded posteroventral margin.

*Occurrences.*—Miocene to Recent sediments along the Japan Sea and the north Pacific areas of Japan (Q5b, M9e, N9a, H9, R9d; see Figure 4).

*Callistocythere kyongjuensis* Huh and Whatley, 1997

Figure 6.9

*Callistocythere kyongjuensis* Huh and Whatley, 1997, p. 32, 34, pl. 1, figs. 1–6.

*Callistocythere* sp. A Huh and Paik, 1992b, pl. 3, fig. 11.

*Remarks.*—This is the first reporting of *C. kyongjuensis* from Japan.

*Occurrences.*—Miocene sediments of the south Japan Sea side areas (M9d, e; see Figure 4).

Genus *Cluthia* Neale, 1973

*Cluthia tamayuensis* Tanaka sp. nov.

Figures 5.2, 6.4, 6.5

*Etymology.*—For the type locality in the town of Tamayu.

*Types.*—Holotype, LV, SUM-CO-1215 (L = 0.41 mm, H = 0.26 mm). Paratypes, RV of male, SUM-CO-1216 (L = 0.39 mm, H = 0.24 mm); RV of female, SUM-CO-1217 (L = 0.41 mm, H = 0.24 mm).

*Type locality.*—Loc. 1–A16.

*Diagnosis.*—valve subreniform. Anterior margin evenly rounded. Surface densely pitted with small, deep, polygonal pits. A mid-ventral carinal ridge runs toward the mid-posterior area. Radial pore canals (10 anteriorly; 10 posteriorly). Significant sexual dimorphism.

*Description.*—Valve subreniform in lateral view. Anterior margin evenly rounded; dorsal margin straight, sloping toward posterior; posterior margin straight (LV), truncate (RV); ventral margin concave. Large sexual dimorphism; in lateral view, male forms more elongate; in dorsal view, female forms inflated laterally. Eye spot not observed. Surface densely pitted with small, deep, polygonal pits. A carinal ridge occupies the mid-ventral area, runs toward the mid-posterior area. One tubercle developed in the posterodorsal area. In dorsal view, carapace appears compressed and subhexagonal; lateral outline sinuate, anterior end more pointed than posterior. In anterior view, carapace subpentagonal, broadest at the carinal ridge; anterior marginal rim strong. Marginal zone narrow, with narrow anterior and posterior vestibula. Marginal pore canals are straight and number 10 anteriorly; 12 ventrally; 10 posteriorly. Selvage well developed. Hinge entomodont: In RV, anterior element is an elliptical tooth; a cremlated median socket lies just below the smooth bar; posterior element is a well-developed toothplate. One very large U-shaped frontal scar. Four adductor scars in a vertical row (the uppermost and lowermost are semicircular, the middle two are elliptical). One semicircular mandibular scar. Two dorsal scars (one elongate dorsomedial; one semicircular mid-dorsal).

*Remarks.*—his species differs from *C. japonica* Tabuki, 1986 from the Plio-Pleistocene Daishaka Formation, northern Japan, in its posterior outline, deep polygonal pits and the carinal ridge toward mid-posterior. The present spe-



cies is distinguished from *C. ishizakii* Zhao, 1988 (MS) from the Late Pleistocene and Holocene drilling cores of the Okinawa Trough, East China Sea (in Ruan and Hao, 1988), in its lateral outline and deep polygonal pits.

*Occurrence*.—Only from the Fujina Formation (M9e; see Figure 4).

*Cluthia subjaponica* Tanaka sp. nov.

Figures 5.3, 6.6, 6.7

*Etymology*.—For its close resemblance with *Cluthia japonica* Tabuki.

*Types*.—olotype, LV of female, SUM-CO-1218 (L = 0.40 mm, H = 0.24 mm). Paratypes, LV of male, SUM-CO-1219 (L = 0.40 mm, H = 0.23mm); LV of female, SUM-CO-1220 (L = 0.40 mm, H = 0.24 mm).

*Type locality*.—Loc. 1-A16.

*Diagnosis*.—Valve subreniform. Anterior margin evenly rounded. Surface densely pitted with small, deep, round pits. Radial pore canals (23 anteriorly; 16 posteriorly). Prominent fulcral point. Sexual dimorphism weak.

*Description*.—Valve subreniform in lateral view. Anterior margin evenly rounded; dorsal margin straight, sloping toward posterior; posterior margin straight; ventral margin nearly straight to slightly convex. Sexual dimorphism weak. Eye spot not observed. Surface densely pitted with small, deep, round pits. One tubercle developed in the posterodorsal area. In dorsal view, lateral outline nearly straight; anterior end more pointed than posterior. In anterior view, LV arched, broadest at point near mid-height; anterior marginal rim strong. Marginal zone relatively broad, with narrow anterior and posterior vestibula. Marginal pore canals are straight, numbering 23 in anterior, 5 in ventral, 16 in posterior. Selvage well developed. Hinge entomodont: in LV, anterior and posterior elements are elongate sockets connected by a containant respectively; a crenulated median bar lies just below the containant. One very large U-shaped frontal scar. Four adductor scars in a vertical row (the uppermost one is semicircular, the lower three are elliptical). One circle mandibular scar. One elliptical dorsal scar mid-dorsally. Prominent fulcral point.

*Remarks*.—This species differs from *C. japonica* Tabuki, 1986 from the Plio-Pleistocene Daishaka Formation, the north Japan, in its lateral outline, small round pits and lack of tubercles in the posterodorsal and posteroventral areas.

*Occurrence*.—Only from the Fujina Formation (M9e; see Figure 4).

Subfamily Schizocytherinae Mandelstam, 1960

Tribe Paijenborchellini Deroo, 1966

Genus *Paijenborchella* Kingma, 1948

*Paijenborchella* cf. *tsurugasakensis* Tabuki, 1986

Figure 7.1, 7.2

*Paijenborchella tsurugasakensis* Tabuki, 1986, p.65–67, pl. 2, figs. 12–19, text-fig. 18–3; Kamiya *et al.*, 1996, pl. 3, fig. 3; Ozawa, 1996, pl. 7, fig. 8.

*Remarks*.—This species was first described from the Plio-Pleistocene Daishaka Formation, the north Japan by Tabuki (1986). Specimens from the Fujina Formation differ slightly from the type specimen, in the shape of posteroventral area.

*Occurrence*.—Miocene to Pleistocene sediments of Japan Sea side areas and northern Honshu, Japan (P5c, M9e and P9d; see Figure 4).

Genus *Palmenella* Hirschmann, 1916

*Palmenella limicola* (Norman, 1865)

Figure 7.3

*Cythere limicola* Norman, 1865a, p. 193; Norman, 1865b, p. 20, pl. 6, figs. 1–4.

*Palmenella limicola* (Norman). Hirschmann, 1916, p. 582–594, text-figs.8–27; Elofson, 1941, p.277, 278, text-fig. 21; Triebel, 1949, p.189, 190, pl. 2, figs. 5, 6; Swain, 1963, p.830, 831, pl.99, figs. 3a–d, text-fig.9d; Ishizaki, 1966, p.156, pl.19, fig. 8; Hanai, 1970, p. 704, text-figs. 6B (solid line), 7G, H; Neale and Howe, 1975, pl. 5, figs. 7, 8; Rosenfeld, 1977, p. 15, 16, pl. 1, figs. 3–6; Lord, 1980, pl. 3, fig. 6; Cronin, 1981, p. 412, pl. 11, figs. 1, 2, 4; Cheong *et al.*, 1986, pl. 2, fig. 1; McDougall *et al.*, 1986, pl. 13, fig. 8; Cronin and Ikeya, 1987, p. 86, pl. 2, fig. 17; Brouwers, 1988, figs. 5, 6; Yajima, 1988, pl. 2, fig. 8; Athersuch *et al.*, 1989, p. 82, 83, pl. 1 (2), fig. 28; Brouwers, 1990, pl. 1, fig. 15, pl. 4, figs. 9, 12, 17, pl. 6, fig. 1; Brouwers *et al.*, 1991, pl. 1, fig. 7; Cronin, 1991, fig. 7–11; Huh and Paik, 1992a, pl. 1, fig. 10; Huh and Paik, 1992b, pl. 1, fig. 10; Hartmann, 1993, p.241, pl. 1, figs. 2–4; Irizuki, 1994, p. 8, pl. 1, fig. 4; Irizuki and Matsubara, 1994, pl. 1, fig. 7; Ozawa *et al.*, 1995, pl. 1, fig. 4; Kamiya *et al.*, 1996, pl. 2, fig. 1; Ozawa, 1996, pl. 7, fig. 9; Irizuki *et al.*, 1998, fig. 5–8; Freiwald and Mostafawi, 1998, pl. 59, fig. 4; (not) Wagner, 1970, pl. 4, fig. 14.

*Kyphocythere limnicola* (Norman). Swain, 1961, fig. 2–20.

*Palmenella* sp. Hanai, 1961, p. 369, text-fig.11, figs. 4a, b.

*Occurrences*.—Miocene to Recent sediments of high-latitude areas (N1, P1a, b, Q1a, b, R2a–e, P3, R3a, c, Q4a, b, M5a, b, P5a, b, H6a, R6a, b, R7a, b, R8, M9b–f, P9d, Q9, R9c; see Figure 4).







Family Hemicytheridae Puri, 1953

Subfamily Urocythereinae Hartmann and Puri, 1974

Genus *Urocythereis* Ruggieri, 1950

*Urocythereis pohangensis* Huh and Whatley, 1997

Figure 7.8

*Urocythereis pohangensis* Huh and Whatley, 1997, p. 36, 37, pl. 2, figs. 3–9.

*Urocythereis* sp. Huh and Paik, 1992a, pl. 1, figs. 17, 18; Huh and Paik, 1992b, pl. 1, figs. 17, 18.

**Remarks.**—This is the first report of *U. pohangensis* from Japan.

**Occurrences.**—Miocene sediments of the south Japan Sea side areas (M9d,e; see Figure 4).

Genus *Laperousecythere* Brouwers, 1993

*Laperousecythere ikeyai* Tanaka sp. nov.

Figures 5.4, 7.4–7.7

**Etymology.**—In honor of N. Ikeya (Shizuoka University, Japan), who is a specialist in the taxonomy and biogeography of the Cenozoic and Recent marine ostracods of the western Pacific region.

**Types.**—Holotype, LV of male, SUM-CO-1225 (L = 0.95 mm, H = 0.51 mm). Paratypes, RV of male, SUM-CO-1226 (L = 0.95 mm, H = 0.49 mm); LV of female, SUM-CO-227 (L = 0.92 mm, H = 0.55 mm); RV of female, SUM-CO-1228 (L = 0.89 mm, H = 0.49 mm); LV of male, SUM-CO-1229 (L = 0.91 mm, H = 0.52 mm).

**Type locality.**—Loc. 1–A15.

**Diagnosis.**—Valve subquadrate. Surface ornamented by polygonal reticulations and a carinal ridge runs nearly parallel to anterior and ventral margin. Vestibule narrow. Four circular/elliptical adductor scars, in three of these the ventral side is subdivided.

**Description.**—Valve subquadrate in lateral view. Anterior margin evenly rounded with infracurvature; dorsal margin straight, sloping gently toward posterior; posterior margin truncated and caudated ventrally; ventral margin nearly straight to slightly convex. Large sexual dimorphism; in lateral view, male forms more elongate; in dorsal

view, the carapaces of female forms are inflated postero-ventrally. Eye spot large and flat. Surface ornamented by polygonal reticulations. A strong carinal ridge occurs at base of eye spot, runs nearly parallel to anterior and ventral margin, and ends at posteroventral area. A subcentral tubercle is developed. In dorsal view, lateral outline nearly straight; anterior end more pointed than posterior. On dorsal surface of carapace a V-shaped groove runs along hinge line (in vertical section). In anterior view, carapace subovate, broadest at point near mid-height. Marginal zone relatively broad, with narrow anterior and posterior vestibula. Marginal pore canals are straight and number 35 in anterior, 17 in posterior, and a few mid-ventrally. Selvage and list well developed. Hinge holamphidont: in LV, anterior element has an auxiliary tooth in a large elongate socket; anteromedian element is a smooth tooth, posteromedian element is a bar; posterior element is an elongate socket. Three frontal scars (the upper two are circular, the lowermost one is elliptical). Four circular/elliptical adductor scars; the three at ventral side are subdivided. A deep anteromedian depression between frontal and adductor scars, corresponding to the external subcentral tubercle. One elliptical mandibular scar. Six dorsal scars (two dorsomedially; two mid-dorsally; two anterodorsally); the uppermost one is semicircular, the others are circular/elliptical. Prominent fulcral point. One semicircular ventral scar is below and anterior to the mandibular scar. Ocular sinus conspicuous. **Remarks.**—This species differs from *L. robusta* (Tabuki, 1986) from the Plio-Pleistocene Daishaka Formation, northern Japan, in its slightly convex ventral margin, polygonal reticulation and lack of secondary reticulations. The present species is distinguished from *L. ishizakii* Irizuki and Matsubara, 1995 from the Early-Middle Miocene Suenomatsuyama Formation, northeast Japan, in its outline and possession of a strong carinal ridge.

**Occurrence.**—Only from the Fujina Formation (M9e; see Figure 4).

Family Trachyleberididae Sylvester-Bradley, 1948

Subfamily Trachyleberidinae Sylvester-Bradley, 1948

Tribe Trachyleberidini Sylvester-Bradley, 1948

Genus *Acanthocythereis* Howe, 1963

◀ **Figure 7.** 1–2, *Paijenborchella* cf. *tsurugasakensis* Tabuki, 1986. 1a: male LV, Loc. 1–A17, SUM-CO-1221; 2a, b: female LV, Loc. 1–A16, SUM-CO-1222; 3: *Palmenella limicola* (Norman, 1865), female LV, Loc. 1–A18, SUM-CO-1223. 4–7, *Laperousecythere ikeyai* Tanaka sp. nov. 4a–e: male LV, holotype, Loc. 1–A15, SUM-CO-1225; 5a–c: male RV, paratype, Loc. 1–A15, SUM-CO-1226; 6a–c: female LV, paratype, Loc. 1–A15, SUM-CO-1227; 7a–c: female RV, paratype, Loc. 1–A15, SUM-CO-1228. 8: *Urocythereis pohangensis* Huh and Whatley, 1997, male LV, Loc. 1–A15, SUM-CO-1224. 9: *Acanthocythereis dunelmensis* (Norman, 1865), female LV, Loc. 2–B4, SUM-CO-1230. 10: *Acanthocythereis koreana* Huh and Whatley, 1997, female LV, Loc. 1–A13, SUM-CO-1240. 11–13, *Acanthocythereis fujinaensis* Tanaka sp. nov. 11a–d: male C. holotype, Loc. 1–A13, SUM-CO-1231; 12a–e: female LV, paratype, Loc. 1–A11, SUM-CO-1232; 13a–c: female RV, paratype, Loc. 1–A11, SUM-CO-1233. Scale bar is 0.10 mm.

*Acanthocythereis dunelmensis* (Norman, 1865)

Figure 7.9

- Cythereis dunelmensis* Norman, 1865a, p. 193; Norman, 1865b, p. 22, pl. 7, figs. 1-4.
- Cythere dunelmensis* (Norman). Brady, 1868, p. 416, pl. 30, figs. 1-12.
- Cythereis dunelmensis* (Norman). Elofson, 1941, p. 296-300, figs. 8-11, text-figs. 29, 30; Elofson, 1943, p. 10; (not) Tressler, 1941, p. 100, pl. 19, fig. 21.
- Trachyleberis dunelmensis* (Norman). Hulings, 1967, p. 324, figs. 7, 8T, pl. 4, figs. 24, 25; Caralp *et al.*, 1967, pl. 13, fig. 1; Caralp *et al.*, 1968, pl. 10, fig. 1.
- Acanthocythereis dunelmensis* (Norman). Neale and Howe, 1975, pl. 1, figs. 3, 11, 13-16; Rosenfeld, 1977, p. 23, 24, pl. 5, figs. 65-68; Lord, 1980, pl. 1, figs. 8-13; Cronin, 1981, p. 400, pl. 8, figs. 1, 2; Cronin, 1986, pl. 2, fig. 9; McDougall *et al.*, 1986, pl. 13, figs. 2-4; Cronin and Ikeya, 1987, pl. 1, figs. 1, 4; Brouwers, 1988, figs. 5-7; Athersuch *et al.*, 1989, p. 133, 134, pl. 3 (10), fig. 52; Cronin, 1989, pl. 2, fig. 9; McKenzie *et al.*, 1989, pl. 1, fig. 1; Hartmann, 1992, pl. 5, figs. 4-6; Ikeya and Suzuki, 1992, pl. 1, fig. 2; Brouwers, 1993, pl. 1, figs. 1-5, pl. 2, fig. 1, pl. 16, fig. 1, text-fig. 3, 4; Irizuki, 1994, p. 10, pl. 2, fig. 3; Irizuki, 1996, figs. 7-1, 2; Kamiya *et al.*, 1996, pl. 2, figs. 8-10; Ozawa, 1996, pl. 1, fig. 1; Freiwald and Mostafawi, 1998, pl. 59, figs. 1, 2.
- Acanthocythereis* cf. *A. dunelmensis* (Norman). Penney, 1993, fig. 5-I.
- ? *Acanthocythereis dunelmensis* (Norman). Cronin and Compton-Gooding, 1987, pl. 2, fig. 4.
- ? *Acanthocythereis* cf. *A. dunelmensis* (Norman). Cronin, 1991, fig. 8-11.
- Cletocythereis dunelmensis dunelmensis* (Norman). Bassiouni, 1965, pl. 2, fig. 8.
- Cletocythereis dunelmensis minor* Bassiouni, 1965, p. 513, 514, pl. 2, fig. 9.
- Actinocythereis* sp., Swain, 1961, fig. 2-36.
- Cletocythereis elofsoni elofsoni* Bassiouni, 1965, p. 514-516, pl. 2, figs. 4, 5.
- Cletocythereis elofsoni elofsoni abbreviata*, Bassiouni, 1965, p. 516, pl. 2, figs. 6, 7.
- Cletocythereis nobilissimus* Swain, 1963, p. 824, 825, pl. 98, fig. 5, pl. 99, figs. 15a, b, text-fig. 10a.
- Acanthocythereis* ? sp. A Cheong *et al.*, 1986, pl. 2, fig. 17.
- Acanthocythereis* ? sp. B Cheong *et al.*, 1986, pl. 2, fig. 18.
- Acanthocythereis* ? sp. C Cheong *et al.*, 1986, pl. 2, fig. 19.
- Trachyleberis* ? *rastrmarginata* (Brady). Swain, 1961, fig. 2-32.

**Occurrences.**—Miocene to Recent sediments of high-latitude areas (R2a-f, P3, R3a, b, d, Q4a-c, P5a, b, Q5a, b, Q6a, H6a, R6a, b, Q7a-e, R7a-d, R8, M9b, N9b, P9a, b, d, R9b, c; see Figure 4).

*Acanthocythereis fujinaensis* Tanaka sp. nov.

Figures 5.5, 7.11-7.13

**Etymology.**—For the type locality.

**Types.**—Holotype, C of male, SUM-CO-1231 (L = 0.41 mm, H = 0.24 mm). Paratypes, LV of female, SUM-CO-1232 (L = 0.43 mm, H = 0.27 mm); RV of female, SUM-CO-1233 (L = 0.42 mm, H = 0.27 mm); LV of female, SUM-CO-1234 (L = 0.46 mm, H = 0.29 mm).

**Type locality.**—Loc. 1-A13.

**Diagnosis.**—Valve subquadrate. Posterior margin evenly rounded. Conical spines developed in the anteroventral margin. Surface ornamented by polygonal reticulations with clavate/conic conjunctive spines.

**Description.**—Valve subquadrate in lateral view. Anterior margin evenly rounded with conical spines, especially anteroventrally; dorsal margin straight, sloping toward posterior with several spines; posterior margin evenly rounded with conical spines posteroventrally; ventral margin concave in male forms, nearly straight in female forms. Strong sexual dimorphism; in lateral view, male forms more elongate; in dorsal view, carapaces of female forms inflated posteroventrally. Eye spot large and protruding. Surface ornamented by polygonal reticulations with clavate/conical conjunctive spines. A row of clavate/conical spines occurs at base of eye spot, runs parallel to anterior margin. Three parallel carinal ridges occupy the mid-ventral area, the uppermost one with clavate spines. A subcentral tubercle developed. In dorsal view, carapace elongate subovate, pointed in front. In anterior view, carapace subovate, lateral outline nearly straight. Marginal zone relatively broad, with very narrow anterior and posterior vestibula. Marginal pore canals are straight/curved with median swellings and number 42 in anterior, 18 in ventral, 23 in posterior. Selvage developed. Hinge holamphidont: in LV, anterior element has an auxiliary tooth in a large elongate socket; anteromedian element is a smooth tooth, posteromedian element is a bar; posterior element is an elongate socket. One U-shaped frontal scar. Four adductor scars in a vertical row (the uppermost one is semicircular, the lower three are elliptical). One elliptical mandibular scar. Three dorsal scars mid-dorsally; the lowermost one protrudes like a tongue, the upper two are elliptical. Prominent fulcral point. One elliptical ventral scar is below and anterior to the mandibular scar. Ocular sinus conspicuous.

**Remarks.**—This species differs from *A. koreana* Huh and Whatley, 1997 from the Miocene, Korea, in its evenly rounded posterior margin, developed anteroventral conical spines and prominent clavate conjunctive spines.

**Occurrence.**—Only from the Fujina Formation (M9e; see Figure 4).



*Acanthocythereis izumoensis* Tanaka sp. nov.

Figures 5.6, 8.1–8.4

*Etymology*.—Izumo is the ancient provincial name of the type locality.

*Types*.—Holotype, LV of male, SUM-CO-1235 (L = 0.92 mm, H = 0.56 mm). Paratypes, RV of male, SUM-CO-1236 (L = 0.91 mm, H = 0.53 mm); LV of female, SUM-CO-1237 (L = 0.90 mm, H = 0.60 mm); RV of female, SUM-CO-1238 (L = 0.92 mm, H = 0.59 mm); LV of female, SUM-CO-1239 (L = 0.90 mm, H = 0.61 mm).

*Type locality*.—Loc. 1–A16.

*Diagnosis*.—Valve subquadrate. In male forms, a large conical spine at the posteroventral corner is prominent. Surface smooth with scattered clavate/conical spines. A row of clavate spines runs parallel to mid-ventral margin. In anterior view, carapace subtrapezoidal, broadest at about one-fifth height from the ventral side. No vestibule.

*Description*.—Valve subquadrate in lateral view. Anterior margin evenly rounded with conical spines, especially anteroventrally; dorsal margin straight, sloping toward posterior with several clavate/conical spines; posterior margin evenly rounded with several conical spines, a large conical spine at the posteroventral corner is more prominent in male forms; ventral margin convex. Strong sexual dimorphism; in lateral view, male forms more elongate; in dorsal view, female forms having inflated carapace in the mid-posterior area. Eye spot large and protruding. Surface smooth with scattered clavate/conical spines. A row of clavate/conical spines occurs at base of the eye spot, runs parallel to anterior margin. A row of clavate spines runs parallel to mid-ventral margin. In dorsal view, carapace elongate subovate, pointed in front. In anterior view, carapace subtrapezoidal, broadest at about one-fifth height from the ventral side. Marginal zone broad; vestibule not developed. Marginal pore canals are straight/curved with median swellings and number 40 in anterior and 20 in posterior. Selvage developed. Hinge holamphidont: in LV, anterior element has an auxiliary tooth in a large elongate socket; anteromedian element is a smooth tooth, posteromedian element is a bar; posterior element is an elongate socket. One V-shaped frontal scar. Four adductor scars in a vertical row (the uppermost and lowermost are semicircular, the middle two are elliptical). One elliptical mandibular scar. Three dorsal scars; the dorsomedian one protrudes like a tongue, the mid-dorsal two are elongate. Prominent fulcral point. One elliptical ventral scar is below and posterior to the mandibular scar. Ocular sinus conspicuous.

*Remarks*.—This species differs from *A. mutsuensis* Ishizaki, 1971 from the Recent sediments of Mutsu Bay in northern Japan, in its row of clavate spines running parallel to the mid-ventral margin. The present species is distin-

guished from *A. koreana* Huh and Whatley, 1997 from the Miocene, Korea, by its smooth surface with scattered clavate/conical spines.

*Occurrence*.—Only from the Fujina Formation (M9e; see Figure 4).

*Acanthocythereis koreana* Huh and Whatley, 1997

Figure 7.10

*Acanthocythereis koreana* Huh and Whatley, 1997, p. 39, pl. 3, figs. 6–12.

*Acanthocythereis mutsuensis* Ishizaki. Huh and Paik, 1992a, pl. 2, figs. 8, 9; Huh and Paik, 1992b, pl. 2, figs. 8, 9.

*Acanthocythereis dunelmensis* (Norman). Irizuki and Matsubara, 1994, pl. 1, fig. 13.

*Occurrences*.—Miocene sediments of the south Japan Sea side areas (M9d, e; see Figure 4).

*Acanthocythereis tsurugasakensis* Tabuki, 1986

Figure 8.5

*Acanthocythereis tsurugasakensis* Tabuki, 1986, p. 85, 86, pl. 11, figs. 2–10, text-fig. 20–2; Ozawa, 1996, pl. 1, fig. 3.

*Occurrences*.—Miocene to Pleistocene sediments along the Japan Sea and Northern Pacific areas of Japan (P5c, M9e and P9d; see Figure 4).

Genus *Robertsonites* Swain, 1963*Robertsonites japonicus* (Ishizaki, 1966)

Figure 8.6

*Buntonia japonica* Ishizaki, 1966, p. 156, 157, pl. 19, figs. 6, 7, text-fig. 1, figs. 1, 5.

*Occurrences*.—Miocene sediments of Honshu, Japan (M9a, e; see Figure 4).

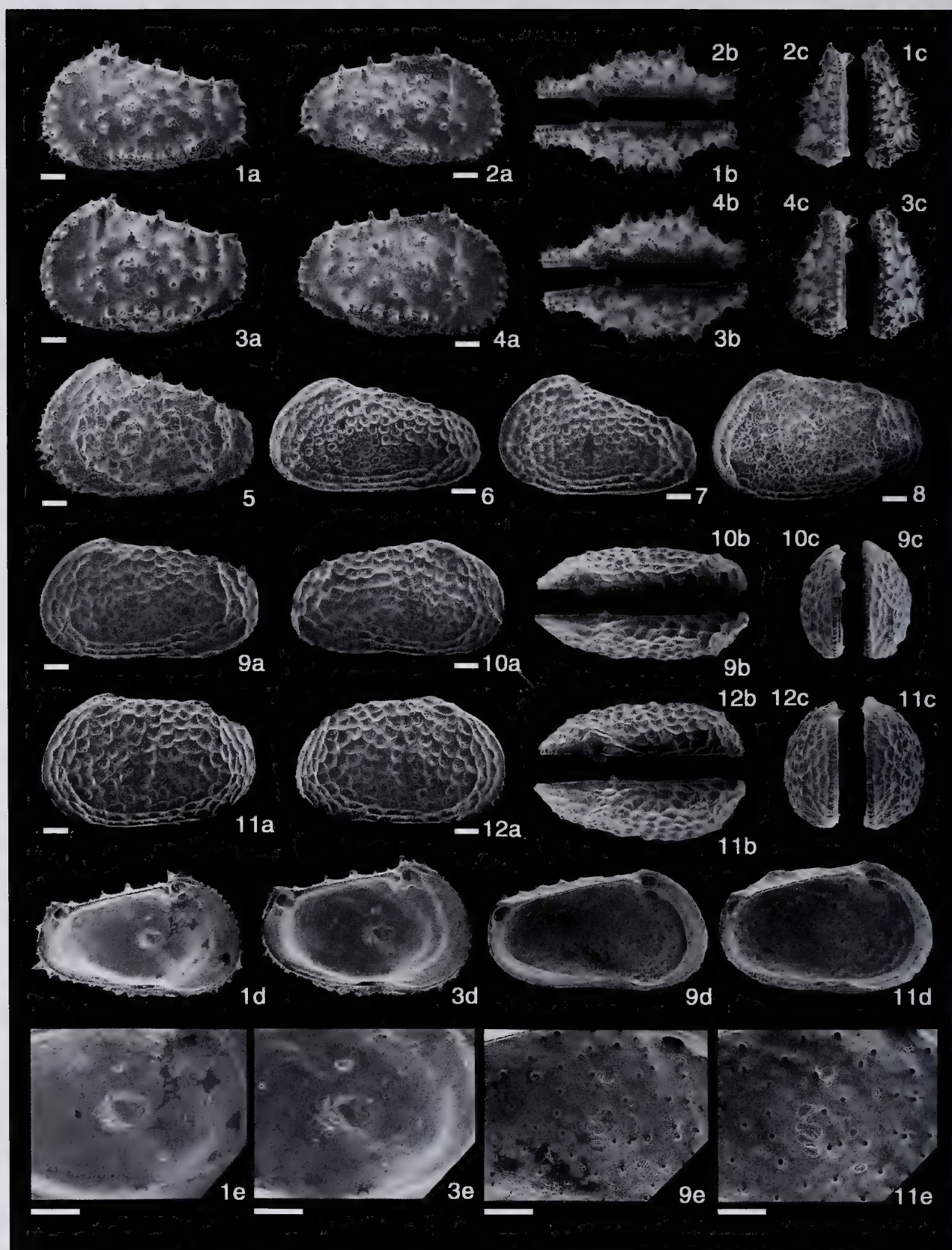
*Robertsonites reticuliformis* (Ishizaki, 1966)

Figure 8.7

*Buntonia reticuliforma* Ishizaki, 1966, p. 157, 158, pl. 16, fig. 7, text-fig. 1, fig. 1; Tabuki, 1986, p. 91–93, pl. 14, figs. 1–12, text-figs. 17–1, 2; Cronin and Ikeya, 1987, p. 84, pl. 2, fig. 15; Yajima and Lord, 1990, fig. 4–9; Huh and Paik, 1992a, b, pl. 2, fig. 13; Irizuki, 1994, p. 10, pl. 2, figs. 4–6; Irizuki, 1996, figs. 7–3, 4; Kamiya *et al.*, 1996, pl. 3, fig. 6; Ozawa, 1996, pl. 8, fig. 6.

*Robertsonites* ? *reticuliforma* (Ishizaki) [sic]. Yajima, 1982, p. 205, pl. 12, fig. 13.







**Remarks.**—This species was first described by Ishizaki (1966) from the Middle Miocene Hatatate Formation in northern Japan. Specimens in Tabuki (1986), Irizuki (1994, 1996), Kamiya *et al.* (1996) and Ozawa (1996) have a prominent posterodorsal subvertical ridge.

**Occurrences.**—Miocene to Pleistocene sediments of Honshu, Japan (P5c, Q5a, b, M9a, b, d, N9b, P9a, c, d, Q9a; see Figure 4).

***Robertsonites* cf. *tuberculatus* (Sars, 1866)**

Figure 8.8

*Cythereis tuberculata* Sars, 1866, p. 37.

*Cythere tuberculata* (Sars). Brady, 1868, p. 406, 407, pl. 30, figs. 25–39.

*Robertsonites tuberculata* (Sars) [sic]. Hulings, 1967, p. 324, pl. 4, figs. 21–23; text-figs. 4e, 8p–8s; Neale and Howe, 1975, p. 419, pl. 1, fig. 1; Rosenfeld, 1977, p. 24, 25, pl. 5, figs. 61–64.

*Robertsonites tuberculatus* (Sars). Cronin, 1981, p. 400, 402, pl. 8, fig. 5; Horne, 1983, p. 39–52, pls. 1–14; Athersuch *et al.*, 1989, p. 148, 149, pl. 4 (7), fig. 59; Cronin, 1989, p. 133, pl. 2, fig. 10; McKenzie *et al.*, 1989, pl. 1, fig. 12; Cronin, 1991, p. 779, fig. 8–2; Hartmann, 1992, p. 187, 188, pl. 5, figs. 7–12; pl. 6, figs. 1–6; Penney, 1993, fig. 5h.

*Robertsonites gubikensis* Swain, 1963, p. 821, 822, pl. 98, figs. 8a, b; pl. 99, fig. 12; text-fig. 9b.

*Robertsonites logani* (Brady and Crosskey). Swain, 1963, p. 823, pl. 97, fig. 13.

*Robertsonites tuberculatina* [sic] Swain, 1963, p. 822, 823, pl. 98, fig. 10; pl. 99, fig. 1; text-fig. 9c.

**Remarks.**—This species exhibits considerable variation in outline and ornament, with variable development of nodes and reticulation (Brouwers, 1993).

**Occurrences.**—Miocene to Recent sediments of high-latitude areas (N1, R2b, f, N3, P3, R3d, Q4b, c, R6a, b, Q7b–e, R7c; see Figure 4).

***Robertsonites yatsukanus* Tanaka sp. nov.**

Figures 5.7, 8.9–8.12

**Etymology.**—The district name of the type locality.

**Types.**—Holotype, LV of male, SUM-CO-1245 (L = 0.95 mm, H = 0.53 mm). Paratypes, RV of male, SUM-

CO-1246 (L = 0.93 mm, H = 0.51 mm); LV of female, SUM-CO-1247 (L = 0.94 mm, H = 0.59 mm); RV of female, SUM-CO-1248 (L = 0.91 mm, H = 0.55 mm); LV of male, SUM-CO-1249 (L = 0.94 mm, H = 0.54 mm).

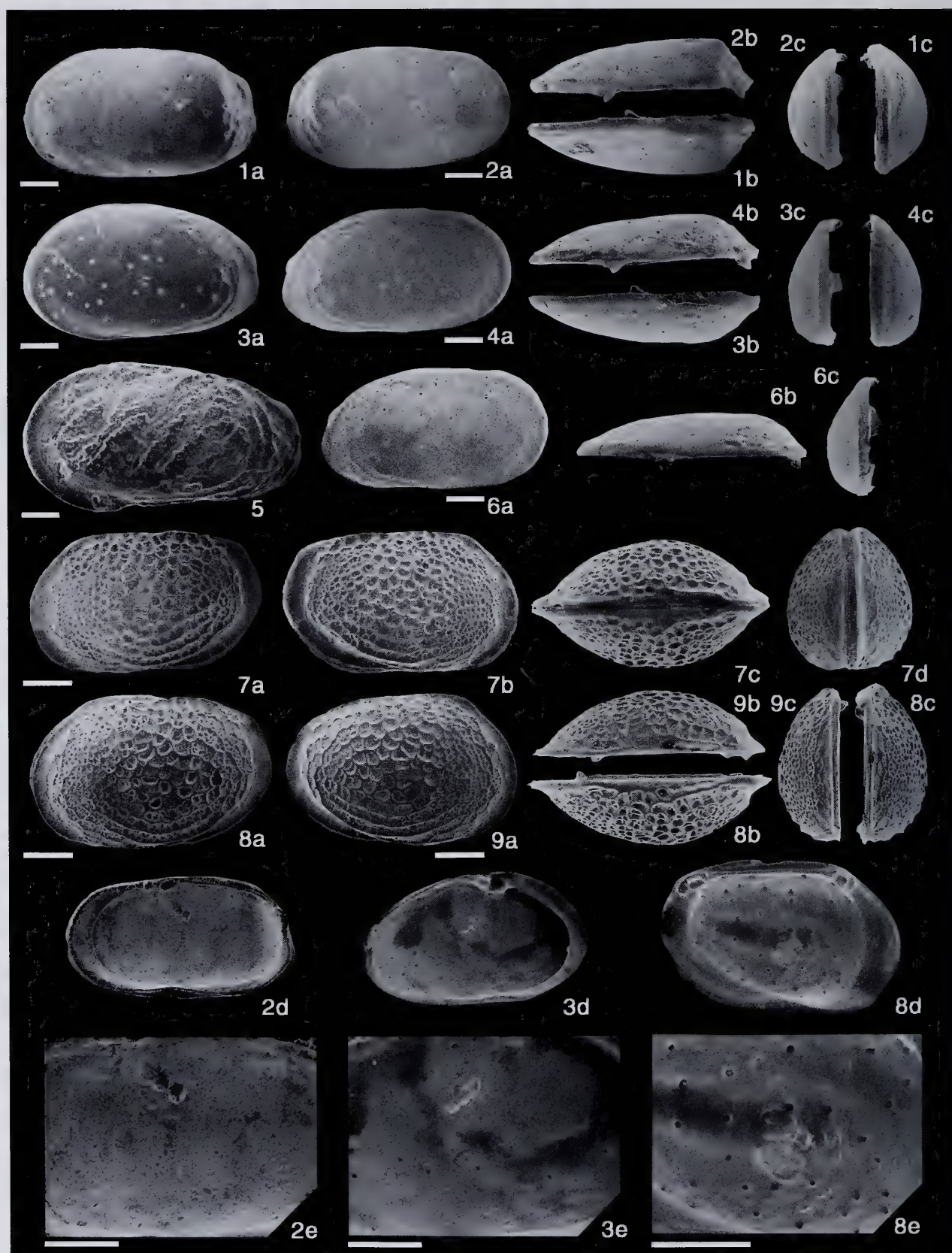
**Type locality.**—Loc. 2–B1.

**Diagnosis.**—Valve quadrate, tapering posteriorly. Surface ornamented by polygonal reticulations. Vestibula developed in the anteroventral area and very narrow in the posteroventral area. One J-shaped frontal scar.

**Description.**—Valve quadrate, tapering posteriorly in lateral view. Anterior margin evenly rounded, weakly denticulated anteroventrally; dorsal margin undulate, sloping toward posterior; posterior margin evenly rounded and weakly denticulated anteroventrally; ventral margin nearly straight. Strong sexual dimorphism; in lateral view, male forms are more elongate; in dorsal view female carapaces are inflated posteriorly. Eye spot small and flat. Surface ornamented by polygonal reticulations. Two anterior carinal ridges prominent, one running from the anterior part of eye spot to the anteroventral area, the other starting at base of eye spot, bifurcating in anterodorsal area and running into anteroventral area. Three carinal ridges run nearly parallel to anterior, ventral and posterior margin and end at posterodorsal area. In dorsal view, carapace is elongate ovate. In dorsal surface of carapace a V-shaped groove runs along hinge line (in a vertical section). In anterior view, carapace subovate, broadest at point near mid-height. Marginal zone relatively broad, vestibula developed in the anteroventral area and very narrow in the posteroventral area. Marginal pore canals straight, number 48 anteriorly, 15 ventrally and 14 posteriorly. Selvage developed. Hinge holamphidont: in LV, anterior element is a large elongate socket; anteromedian element is a tongue like tooth, posteromedian element is a bar; posterior element is an elongate socket. One J-shaped frontal scar. Four adductor scars in a vertical row (the uppermost and lowermost are semicircular, the middle two are narrow). One elliptical mandibular scar. Eight dorsal scars (five dorsomedially; two mid-dorsally; one anterodorsally); the dorsomedian one protrude like a tongue, the others are circular/elliptical. Fulcral point not observed. One elliptical ventral scar is below and posterior to the mandibular scar. Ocular sinus conspicuous.

**Remarks.**—This species differs from *R. hanaii* Tabuki, 1986 from the Plio-Pleistocene Daishaka Formation in

Figure 8. 1–4, *Acanthocythereis izumoensis* Tanaka sp. nov. 1a–e: male LV, holotype, Loc. 1–A16, SUM-CO-1235; 2a–e: male RV, paratype, Loc. 1–A16, SUM-CO-1236; 3a–c: female LV, paratype, Loc. 1–A16, SUM-CO-1237; 4a–c: female RV, paratype, Loc. 1–A17, SUM-CO-1238. 5: *Acanthocythereis tsurugasakensis* Tabuki, 1986, female LV, Loc. 2 B2, SUM-CO 1241. 6: *Robertsonites japonicus* (Ishizaki, 1966), male LV, Loc. 1–A11, SUM-CO-1242. 7: *Robertsonites reticuliformis* (Ishizaki, 1966), male LV, Loc. 1–A15, SUM-CO-1243. 8: *Robertsonites* cf. *tuberculatus* (Sars, 1866), female LV, Loc. 2–B4, SUM-CO-1244. 9–12, *Robertsonites yatsukanus* Tanaka sp. nov. 9a–e: male LV, holotype, Loc. 2–B1, SUM-CO-1245; 10a–c: male RV, paratype, Loc. 2–B1, SUM-CO-1246; 11a–e: female LV, paratype, Loc. 2–B1, SUM-CO-1247; 12a–c: female RV, paratype, Loc. 2–B1, SUM-CO-1248. Scale bar is 0.10 mm.





northern Japan, in its inflated carapace and three carinal ridges running nearly parallel to anterior, ventral and posterior margins. *R. yatsukanus* is distinguished from *R. tsugaruana* [sic] Tabuki, 1986 from the Plio-Pleistocene Daishaka Formation in northern Japan, in lack of secondary reticulations.

**Occurrence.**—Only from the Fujina Formation (M9e; see Figure 4).

Subfamily Buntoniinae Apostolescu, 1961  
Genus *Ambtonia* Malz, 1982

*Ambtonia shimanensis* Tanaka sp. nov.

Figures 5.8, 9.1, 9.2

**Etymology.**—The prefecture name, Shimane, of the type locality.

**Types.**—Holotype, RV, SUM-CO-1250 (L = 0.61 mm, H = 0.33 mm). Paratypes, LV, SUM-CO-1251 (L = 0.63 mm, H = 0.35 mm); LV, SUM-CO-1252 (L = 0.65 mm, H = 0.36 mm).

**Type locality.**—Loc. 1-A11.

**Diagnosis.**—Valve subcylindrical. Dorsal margin nearly straight. In dorsal view, carapace elongately arrowhead-shaped, tapered in front. Maximum width about one-sixth length from the posterior end. In anterior view, carapace subovate, broadest near mid-height. One V-shaped frontal scar.

**Description.**—Valve subcylindrical in lateral view. Anterior margin evenly rounded; dorsal margin nearly straight; truncated and caudate ventrally; ventral margin nearly straight to slightly convex. Sexual dimorphism unknown. Eye spot not observed. Surface smooth, scattered deep punctations which are the openings of normal pore canals. Anterior area compressed along the anterior margin. In dorsal view, carapace elongately arrowhead-shaped, tapered in front. Maximum width at about one-sixth length from the posterior end. In anterior view, carapace subovate, broadest at point near mid-height. Marginal zone broad in the anterior area, vestibula developed in the anteroventral area and very narrow in the posteroventral area. Marginal pore canals are straight and number 39 anteriorly, 7 ventrally and 11 posteriorly. Selvage and list well developed. Hinge hemiamphidont: in LV, anterior element has a large elongate socket; anteromedian element is a smooth elongate tooth, postero-median element is a crenulate bar; posterior element is an

elongate socket with several lobes dorsally. One V-shaped frontal scar. Four elliptical adductor scars in a vertical row, the middle two of which are narrow. One elliptical mandibular scar. Two dorsal scars protrude like pivots in the dorsomedian area. Fulcral point not observed. One small round ventral scar is below and posterior to the mandibular scar. No ocular sinus.

**Remarks.**—This species differs from *A. obai* (Ishizaki, 1971) from the Recent sediments of Mutsu Bay in northern Japan, in its caudate posteroventral margin, slightly convex ventral margin and compressed anterior area. The present species is distinguished from *A. tongassensis* Brouwers, 1993 from the Quaternary sediments of the Gulf of Alaska, North America, in its caudated posteroventral margin, nearly parallel dorsal and ventral margins, and number of marginal pore canals. This species differs from *A. glabra* Malz, 1982 from the Plio-Pleistocene Ssukou Formation of southwest Taiwan, in its straight dorsal margin.

**Occurrence.**—Only from the Fujina Formation (M9e; see Figure 4).

*Ambtonia takayasui* Tanaka sp. nov.

Figures 5.9, 9.3, 9.4, 9.6

*Falsobuntonia taiwanica* Malz. Yajima, 1988, pl. 1, fig. 7; Huh and Paik, 1992b, pl. 2, fig. 14.

*Ambtonia obai* (Ishizaki). Huh and Paik, 1992a, pl. 2, fig. 14.

**Etymology.**—In honor of K. Takayasu (Center for Coastal Lagoon Environments of Shimane University, Japan), who is a specialist in the taxonomy and paleoecology of the molluscs of the Fujina Formation.

**Types.**—Holotype, LV of female, SUM-CO-1253 (L = 0.64 mm, H = 0.37 mm). Paratypes, RV of female, SUM-CO-1254 (L = 0.63 mm, H = 0.33 mm); RV of male, SUM-CO-1255 (L = 0.62 mm, H = 0.33 mm); LV of female, SUM-CO-1256 (L = 0.64 mm, H = 0.37 mm).

**Type locality.**—Loc. 1-A16.

**Diagnosis.**—Valve subcylindrical. Dorsal margin arched. In dorsal view, carapace elongately arrowhead-shaped, tapered in front. Maximum width about one-fifth length from the posterior end. In anterior view, carapace subpentagonal, lateral outline nearly straight. One J-shaped frontal scar.

**Description.**—Valve subcylindrical in lateral view. Anterior margin evenly rounded; dorsal margin arched; posterior margin truncated and caudated ventrally; ventral

Figure 9. 1-2, *Ambtonia shimanensis* Tanaka sp. nov. 1a-c: LV, paratype, Loc. 1-A11, SUM-CO-1251; 2a-e: RV, holotype, Loc. 1-A11, SUM-CO-1250. 3-4, 6, *Ambtonia takayasui* Tanaka sp. nov. 3a-e: female LV, holotype, Loc. 1-A16, SUM-CO-1253; 4a-c: female RV, paratype, Loc. 1-A16, SUM-CO-1254; 6a-c: male RV, paratype, Loc. 1-A11, SUM-CO-1255. 5: *Falsobuntonia taiwanica* Malz, 1982, male LV, Loc. 1-A20, SUM-CO-1257. 7-9, *Palmoconcha irizukii* Tanaka sp. nov. 7a-d: male C, holotype, Loc. 1-A15, SUM-CO-1258; 8a-e: female LV, paratype, Loc. 1-A15, SUM-CO-1259; 9a-c: female RV, paratype, Loc. 1-A15, SUM-CO-1260. Scale bar is 0.10 mm.

margin straight. Weak sexual dimorphism. Eye spot not observed. Surface smooth; scattered deep punctations, which are the openings of normal pore canals. Anterior area compressed along the anterior margin. Three weak muri run parallel to posterior margin in the posterior area. In dorsal view, carapace elongately arrowhead-shaped, tapered in front. Maximum width about one-fifth length from the posterior end. In anterior view, carapace subpentagonal, lateral outline nearly straight. Marginal zone broad in the anterior area, vestibula developed in the anteroventral area and very narrow in the posteroventral area. Marginal pore canals straight, number 39 anteriorly, 6 ventrally and 15 posteriorly. Selvage and list well developed. Hinge hemiamphidont: in LV, anterior element has a large elongate socket; anteromedian element is a smooth elongate tooth, posteromedian element is a crenulate bar; posterior element is an elongate socket with several lobes dorsally. One J-shaped frontal scar. Four elliptical adductor scars in a vertical row, the middle two are narrow. One round mandibular scar. Two dorsal scars protrude like pivots in the dorsomedian area. Fulcral point not observed. One small round ventral scar is below and posterior to the mandibular scar. No ocular sinus.

**Remarks.**—This species differs from *A. tongassensis* Brouwers, 1993 from the Quaternary sediments of the Gulf of Alaska, North America, in its outline in lateral view.

**Occurrence.**—Miocene formations from Japan and Korea (M9d, e, g; see Figure 4).

#### *Falsobuntonia taiwanica* Malz, 1982

Figure 9.5

*Falsobuntonia taiwanica* Malz, 1982, p. 392, 393, pl. 8, figs. 51–56; Huh and Paik, 1992a, pl. 2, fig. 15; Huh and Paik, 1992b, p. 111, pl. 2, fig. 15; (non) Yajima, 1988, pl. 1, fig. 7; Huh and Paik, 1992b, p. 111, pl. 2, fig. 14.

**Occurrences.**—Miocene to Pleistocene sediments of Japan, Korea and Taiwan (M9d, e and P9e; see Figure 4).

Family Loxoconchidae Sars, 1926

Genus *Palmoconcha* Swain and Gilby, 1974

#### *Palmoconcha irizukii* Tanaka sp. nov.

Figures 5.10, 9.7–9.9

*Palmoconcha* sp. Irizuki and Matsubara, 1994, pl. 1, fig. 19.

**Etymology.**—In honor of T. Irizuki (Aichi University of Education, Japan) who is a specialist in the study of Cenozoic fossil ostracod assemblages of Japan. **Types.**—Holotype, C of male, SUM-CO-1258 (L = 0.47 mm, H = 0.28 mm). Paratypes, LV of female, SUM-CO-1259 (L =

0.49 mm, H = 0.31 mm); RV of female, SUM-CO-1260 (L = 0.46 mm, H = 0.31 mm); LV of female, SUM-CO-1261 (L = 0.51 mm, H = 0.34 mm).

**Type locality.**—Loc. 1–A15.

**Diagnosis.**—Valve rhomboidal. Surface ornamented by punctations in the anterior area. Three concentric muri occur in the anteroventral area, convex ventrally in the mid-ventral area, ends in mid-posterior area. One prominent murus runs from the mid-dorsal area to the posterodorsal area, arched dorsally. One large U-shaped frontal scar.

**Description.**—Valve rhomboidal in lateral view. Anterior margin evenly rounded; dorsal and ventral margins straight in male forms, arched in female forms; posterior margin truncated obliquely in upper half and lower half making blunt angle slightly above mid-height. Strong sexual dimorphism; in lateral view, male forms more elongate; in dorsal view, carapaces of female forms inflated in lateral outline. Eye spot not observed. Surface ornamented by punctations in the anterior area, polygonal reticulations and secondary reticulations in the median and posterior areas. Three concentric muri occur in the anteroventral area, convex ventrally in the mid-ventral area, ends at mid-posterior area. One prominent murus runs from the mid-dorsal area to the posterodorsal area, arched dorsally. In dorsal view, carapace ovate, widest at mid-length, pointed at the anterior and posterior ends. In anterior view, carapace subovate, broadest a little below mid-height. Marginal zone broad anteriorly and posteriorly, with developed vestibula. Marginal pore canals straight, number 6 anteriorly, 11 ventrally, 6 posteriorly. Selvage and list well developed. Hinge gongylodont: In LV, anterior element is a downturned claw-shaped ridge around a socket; median element is a smooth bar; posterior element is a horseshoe-shaped socket around a ball-like knob. One large U-shaped frontal scar. Four adductor scars in a vertical row (the upper three are elliptical, the lowermost one is semicircular). Two elliptical mandibular scars. Five elliptical dorsomedian dorsal scars. Prominent fulcral point.

**Remarks.**—This species differs from *Loxoconcha* (*Palmoconcha*) *parapontica* Zhou, 1995 from the Recent sediments of Kumano-nada and Hyuga-nada, southwest Japan, in its anterior marginal outline and punctations in the anterior area. *P. irizukii* is distinguished from *P. saboyamensis* (Ishizaki, 1966) from the Middle Miocene Hatatate Formation of northeast Japan, in the outline of the anterior margin and the three concentric muri running toward the mid-posterior area.

**Occurrences.**—Middle Miocene sediments, Honshu, Japan (M5a and M9e; see Figure 4).

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# Stratigraphic and palaeoenvironmental significance of a Pennsylvanian (Upper Carboniferous) palynoflora from the Piauí Formation, Parnaíba Basin, northeastern Brazil

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**Abstract.** A well-preserved palynoflora is reported from within a cored interval of a coal-exploratory borehole (1-UN-23-PI of the Geological Survey of Brazil) in the southern part of the Parnaíba Basin, northeastern Brazil. The sample studied is from the lower portion of the Piauí Formation. Its palynoflora is characterized by particular abundance of the trilete cavate/pseudosaccate miospores *Spelaotriletes triangulus* Neves and Owens, 1966 and *S. arenaceus* Neves and Owens, 1966, together with cingulizonate forms mainly attributable to *Vallatisporites* Hacquebard, 1957 and *Cristatisporites* R. Potonié and Kremp emend. Butterworth *et al.*, 1964. Radially and bilaterally symmetrical monosaccate pollen grains are also well-represented, chiefly by *Plicatipollenites* Lele, 1964 and *Potoniopsisporites* Bhardwaj, 1954, respectively. Taeniate grains (i.e., monosaccates and bisaccates) are relatively minor constituents of the palynoflora; no marine microplankton were encountered. Several species are described in detail: the trilete apiculate spores *Brevitriletes levis* (Balme and Hennelly) Bharadwaj and Srivastava, 1969 and *Horriditriletes uruguaiensis* (Marques-Toigo) Archangelsky and Gamero, 1979; and the taeniate pollen grains *Meristocarpus ostentus* sp. nov. and *Lahirités segmentatus* sp. nov. A Pennsylvanian (Late Carboniferous: late Westphalian) age is adduced for the palynoflora via its correlation with part of the Tapajós Group (specifically, the upper Itaituba Formation) of the Amazonas Basin in northern Brazil. The entirely land-derived palynomorphs, associated with abundant plant debris, corroborate previous suggestions that the lower part of the Piauí Formation accumulated in a nonmarine setting under conditions of aridity.

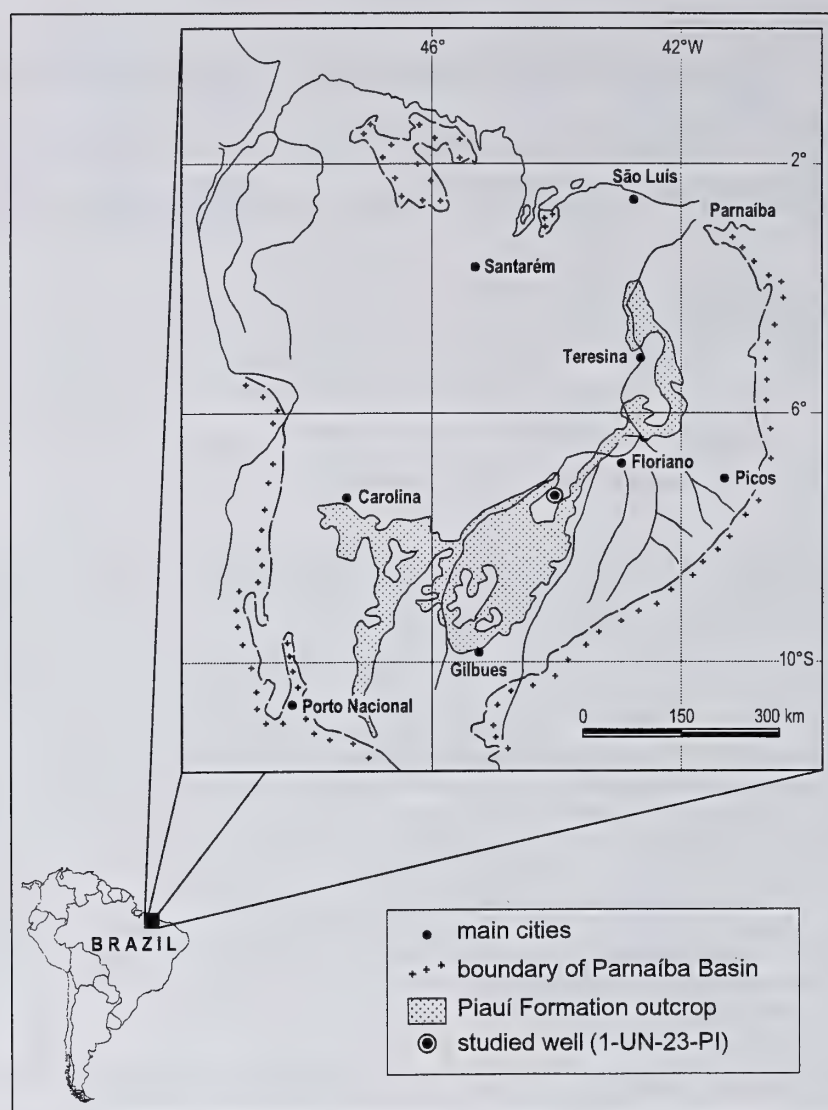
**Key words:** biostratigraphy, Brazil, Pennsylvanian, palynology, Parnaíba Basin, Piauí Formation

## Introduction

The Carboniferous-Permian rocks of the Palaeozoic basins in north and northeast Brazil provide excellent regional source and reservoir systems for liquid petroleum and gas. Palynology has been applied successfully as a basis for biostratigraphic subdivision of these upper Palaeozoic sequences, although the carbonate and evaporite intervals therein are normally only sparsely, if at all, palyniferous. In the Parnaíba Basin (Figure 1), the Balsas Group, with the Piauí Formation at its base, comprises these younger Palaeozoic deposits. During the Balsas tectonic-depositional cycle, the Parnaíba Basin experienced conditions of severe aridity, and received predominantly continental deposits (Cunha, 1986; Lima Filho, 1991). Lithologies are mainly of sandy, evaporitic, and muddy character and clearly reflect strongly oxidizing conditions of deposition.

Such factors obviously tend to militate against their palynostratigraphic potentialities. Accordingly, only a few palynological investigations have been conducted on upper Palaeozoic strata of the Parnaíba Basin. Inferences about age and palaeoenvironment (Müller, 1962) were based on material from exploratory wells drilled by Petrobras. At the beginning of the 1970s, the National Department of Mineral Production (DNPM) initiated research on coal encountered in several wells drilled close to the basin border, but no biostratigraphic analyses were undertaken. The present study concerns the lower part of the Balsas Group, viz., the Piauí Formation, as intersected in one of the DNPM wells. The aims are to determine the chronostratigraphic position of the strata, their possible correlation with other Brazilian Palaeozoic basins, and their environment of deposition.

The section of the 1-UN-23-PI well, investigated herein,



**Figure 1.** Locality map, Parnaíba Basin, northeastern Brazil, indicating site of borehole (1-UN-23-PI of the Geological Survey of Brazil) sampled for this study.

provides the first spore-pollen inventory for the lower part of the Piauí Formation. Obviously, a comprehensive palynological evaluation of the whole formation would necessarily be based on systematic sampling through the vertical extent of the formation, as developed in the subsurface and in outcrop.

As discussed subsequently, the identified spore-pollen assemblage can be compared, for purposes of stratal correlation, with those that characterize palynostratigraphic units established elsewhere; particularly the Upper Carboniferous-Permian palynozones defined in the Tapajós Group of the Amazonas Basin, northern Brazil (Playford and Dino, 2000b). Palaeoenvironmental implications of the Piauí palynoflora are somewhat limited, and are considered

in concert with physical evidence advanced by previous workers.

### Outline of stratigraphy

The Parnaíba Basin is essentially a Palaeozoic basin, but includes a cover of younger (Mesozoic and Cenozoic) strata. It is a substantial intracratonic entity, occupying some 600,000 km<sup>2</sup> in the western part of Brazil's northeastern region and positioned among fold belts that border the Guaporé, São Luiz, and San Francisco cratons. Total stratal thickness is *ca.* 3500 m, of which 2900 m comprise Palaeozoic sediments and the remainder are Mesozoic and Cenozoic deposits. The basin's Palaeozoic succession is divi-



sible into three major sedimentary cycles related to different tectonic, structural, and climatic circumstances. In ascending order, these cycles are manifested lithostratigraphically by what are termed the Serra Grande, Canindé, and Balsas Groups.

The initial cycle, of Silurian age, began with the tectonic-thermal development of a large depression in which fluvial, deltaic, and shallow marine sediments of the Serra Grande Group accumulated (Cunha, 1986; Góes and Feijó, 1994). With continuing tectonic evolution, the Canindé Group (of the second cycle) was deposited during Devonian-Early Carboniferous time. This consists of deltaic and shallow marine to paralic deposits at the base, grading upwards into fluvial-deltaics and periglacial, and culminating with fluvial-deltaic and storm-related deposits. The final (Balsas) Palaeozoic cycle in the basin commenced in the Pennsylvanian and extended through the Permian until earliest Triassic time. It followed pronounced uplift that exposed and eroded much of the Brazilian, indeed South American, platform. Accordingly, the Parnaíba Basin experienced strong erosion, as evidenced by its extensive and well-developed pre-Balsas unconformity. Moreover, the climate changed markedly: from the temperate and humid climates of the preceding cycles to conditions characterized by increasing heat and aridity (Mesner and Wooldridge, 1962, 1964). The sediments of this third phase signify dominantly continental conditions, with occasional marine incursions that became increasingly evaporitic.

### Piauí Formation

The term Piauí was introduced by Small (1914) to designate—as “Série Piauí”—the entire Palaeozoic section of the Parnaíba Basin. Its application was later restricted (Duarte, 1936) to constitute—as the Piauí Formation—the lowest of four formations that embody the basin’s youngest Palaeozoic sedimentary cycle (Balsas Group). This usage is still widely accepted and is adopted herein. The Piauí Formation is a predominantly clastic sedimentary unit, developed widely in the Parnaíba Basin and resting unconformably upon the Canindé Group. The formation crops out in a broad, almost continuous strip along the eastern and southern margins of the basin and discontinuously to the west (Andrade and Daemon, 1974; Suguio and Fulfaro, 1977). Its maximum thickness of *ca.* 350 m is encountered in the subsurface.

Mesner and Wooldridge (1964) proposed a twofold subdivision of the Piauí Formation. The lower part consists of pink to red sandstone; the upper part comprises alternating green and red shales, thin anhydrite beds, pink dolomite, and red or pale grey carbonate beds containing marine fossils. Lima Filho (1991), while maintaining the binary subdivision, modified slightly the Piauí Formation’s limits. He recognized several depositional systems in the forma-

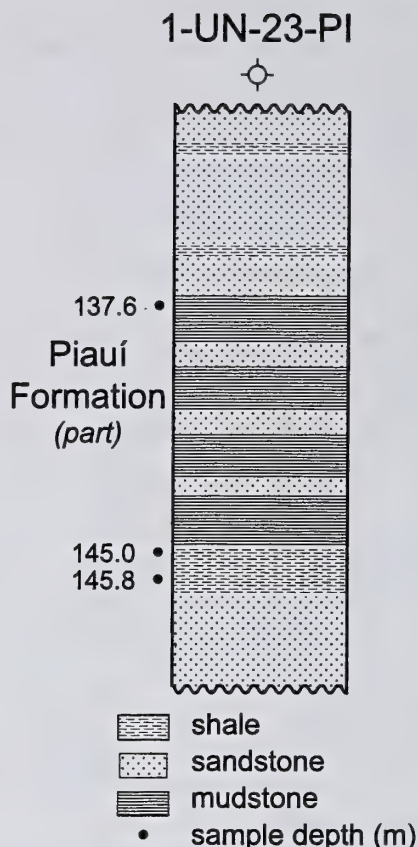
tion, in particular citing evidence of aeolian and deltaic sedimentation and, towards the top, an episode of shallow marine, carbonate deposition. Accordingly, Lima Filho (1991) concluded that the Piauí Formation accumulated under arid conditions in a setting that included an extensive interior desert and an evaporitic marine basin.

The Piauí Formation consists chiefly of continental redbeds, aeolian sandstones, and fluvial deposits. However, brief marine incursions are attested by the presence of richly fossiliferous carbonate platform or lagoonal sediments, particularly in the formation’s upper part as developed in the basin’s northeastern sector. Known locally by such names as Mocambo, Contendas, Meruoca, Carimã, Vidalgo, and Boa Esperança, these marine strata become increasingly evaporitic upsection, providing evidence of progressive aridity. The marine faunas, though mostly undescribed, are diverse. They include bivalves, gastropods, cephalopods, brachiopods, trilobites, bryozoans, and echinoderms (crinoids especially), together with conodonts, agglutinated and calcareous Foraminifera, ostracodes, micro-molluscs, and other microfossils (see Duarte, 1936; Kegel, 1951; Kegel and Costa, 1951; Mesner and Wooldridge, 1964; Campanha and Rocha Campos, 1979; Assis, 1980). Faunal affinities between the Piauí Formation and the Itaituba Formation of the Amazonas Basin—as noted by such authors as Mendes (1966), Tengan *et al.* (1976), Campanha and Rocha Campos (1979), and Assis (1980)—support the hypothesis of a marine connection between the Parnaíba and Amazonas Basins during Pennsylvanian time.

### Material and methods

This study is based on material from a continuously cored well designated as 1-UN-23-PI and located in the state of Piauí, municipal district of Antonio Almeida, at latitude 7° 15′ 18″ South, longitude 44° 12′ 24″ West, in the southern Parnaíba Basin (Figure 1). Three samples were collected from the depth interval 137.6–145.8 m, representative of the top of the Piauí Formation’s lower portion (Figure 2). Of these samples, only one (a grey siltstone, at 145.0 m) proved palyniferous, yielding an abundant and well-preserved palynoflora. The two unproductive samples, collected at depths of 137.6 m and 145.8 m, are both greenish grey shales.

Conventional physico-chemical methods were applied in the laboratory preparation of the samples, specifically those outlined in Playford and Dino (2000a, p. 10–12). Light-microscope photographs of palynomorphs were taken with a Zeiss MC 80 DX camera coupled with a Zeiss Axioplan microscope using Kodak T-Max (100 ASA) film. Scanning electron microscopy assisted in the identification of several species.



**Figure 2.** Portion of 1-UN-23-PI litholog showing palynologically sampled interval of Piauí Formation.

### Composition of palynoflora

The palynoflora recovered from the productive Piauí sample is dominated by pteridophytic trilete spores and gymnospermous monosaccate pollen grains occurring in almost equal proportions (each accounting for ca. 45% of the total assemblage). Taeniate bisaccate grains are relatively minor constituents (ca. 7%). In addition, fresh or brackish water green algae (*Botryococcus*, *Brazilea*) have been recovered. No palaeomicroplanktic elements were encountered.

Given below is an inventory of all palynomorph taxa identified. The large majority of these are illustrated by light micrographs (Figures 3, 5–8) and a few also by scanning electron micrographs (Figures 4, 9). In the system-

atic section, four species (asterisked hereunder) are described in detail, and brief notes are appended on discrimination of the two *Spelaeotriletes* species encountered. Illustrated specimens are listed in relevant figure captions with slide number followed by microscope-stage coordinates (per standard "England Finder" slide). Permanent repository of the specimens is Petrobras/Cenpes/Divex/Sebipec, Cidade Universitária, Quadra 7, Ilha do Fundão, 21949-900 Rio de Janeiro, RJ, Brazil.

### Spores

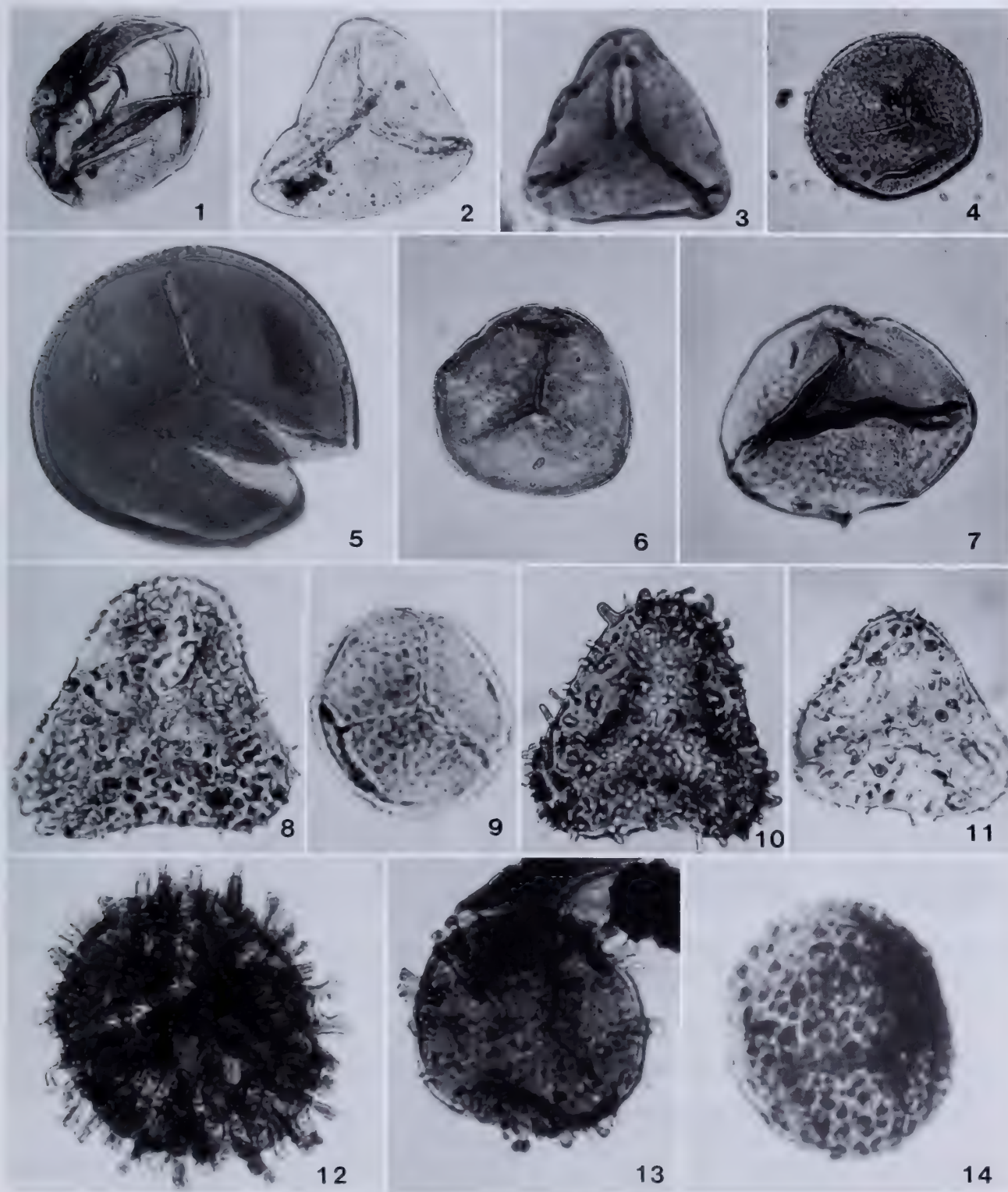
- Anteturma Proximegerminantes R. Potonié, 1970
- Turma Triletes Reinsch emend. Dettmann, 1963
- Suprasubturma Acavatitriletes Dettmann, 1963
- Subturma Azonotriletes Lubert emend. Dettmann, 1963
- Infraturma Laevigati Bennie and Kidston emend. R. Potonié, 1956
- Leiotriletes* sp. [Figure 3.7]
- Calamospora* sp. cf. *C. sinuosa* Leschik, 1955 [Figure 3.1]
- Punctatisporites gretensis* Balme and Hennelly, 1956 [Figure 3.5]
- Punctatisporites* sp. [Figure 3.6]
- Infraturma Apiculati Bennie and Kidston emend. R. Potonié, 1956
- Subinfraturma Granulati Dybová and Jachowicz, 1957
- Granulatisporites austroamericanus* Archangelsky and Gamero, 1979 [Figures 3.2, 3.3, 4.1]
- Cyclogranisporites minutus* Bhardwaj, 1957 [Figure 3.4]
- Subinfraturma Nodati Dybová and Jachowicz, 1957
- "*Acanthotriletes*" *menendezii* Gonzales-Amicon, 1973 [Figure 3.8]
- \**Brevitriletes levis* (Balme and Hennelly) Bharadwaj and Srivastava, 1969 [Figure 3.9]
- Subinfraturma Baculati Dybová and Jachowicz, 1957
- Horriditriletes ramosus* (Balme and Hennelly) Bharadwaj and Saluja, 1964 [Figures 3.11, 4.2]
- \**Horriditriletes uruguiensis* (Marques-Toigo) Archangelsky and Gamero, 1979 [Figures 3.10, 4.3, 4.4]
- Baculatisporites* sp.
- Raistrickia cephalata* Bharadwaj, Kar, and Navale, 1976 [Figures 3.12, 9.3]
- Raistrickia* sp. cf. *R. saetosa* (Loose) Schopf, Wilson, and Bentall, 1944 [Figure 3.13]
- Raistrickia* sp.
- Subinfraturma Verrucati Dybová and Jachowicz, 1957

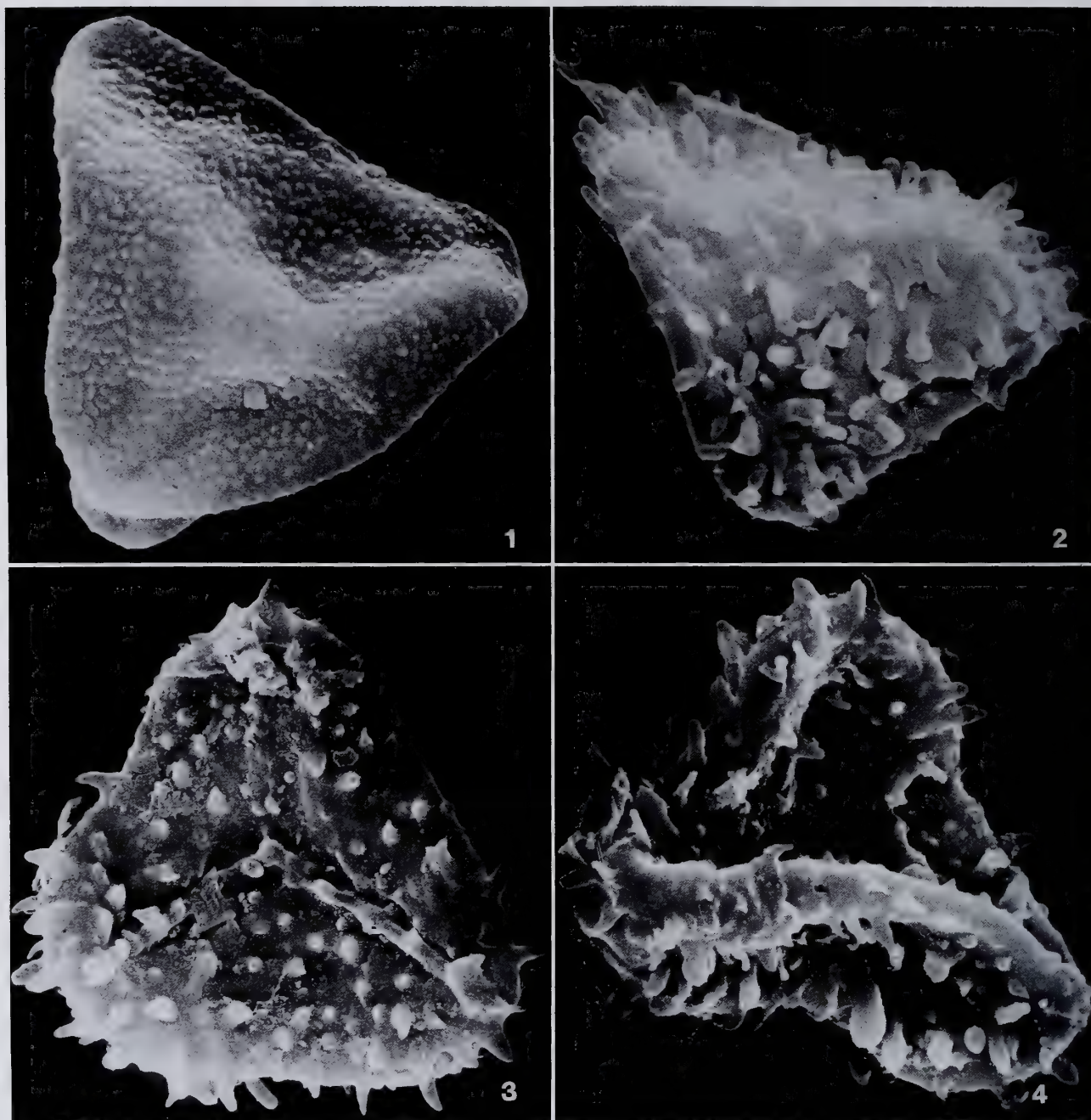
→ **Figure 3.** 1. *Calamospora* sp. cf. *C. sinuosa*, ×500, 20005916E, K/42. 2, 3. *Granulatisporites austroamericanus*; 2, ×750, 20005916/3, Y45/2; 3, ×750, 20005916/3, R51. 4. *Cyclogranisporites minutus*, ×750, 20005916D, M36/3. 5. *Punctatisporites gretensis*, ×750, 20005916E, M49/2. 6. *Punctatisporites* sp., ×500, 20005916D, P55. 7. *Leiotriletes* sp., ×750, 20005916B, N39/2. 8. "*Acanthotriletes*" *menendezii*, ×1000, 20005916D, H39. 9. *Brevitriletes levis*, ×750, 20005916/1, A64/3. 10. *Horriditriletes uruguiensis*, ×1000, 20005916D, O38/1. 11. *Horriditriletes ramosus*, ×500, 20005916D, W48/3. 12. *Raistrickia cephalata*, ×750, 20005916E, V50/3. 13. *Raistrickia* sp. cf. *R. saetosa*, ×750, 20005916/1, B57. 14. *Verrucosiporites* sp. cf. *V. morulatus*, ×750, 20005916/2, U66.



*Verrucosisporites andersonii* Backhouse, 1988 [Figure 5.1, 5.2]  
*Verrucosisporites* sp. cf. *V. morulatus* (Knox) Smith and

Butterworth, 1967 [Figure 3.14]  
 Suprasubturma Laminatitriletes Smith and Butterworth, 1967





**Figure 4.** 1. *Granulatisporites austroamericanus*,  $\times 1900$ , 20005916/S1, S41/2. 2. *Horriditriteles ramosus*,  $\times 2000$ , 20005916/S1, S42. 3, 4. *Horriditriteles uruguayensis*; 3,  $\times 1900$ , 20005916/S1, Q41; 4,  $\times 2300$ , 20005916/S1, N39.

Subturma Zonolaminatitriteles Smith and Butterworth, 1967

Infraturma Cingulicavati Smith and Butterworth, 1967

*Vallatisporites arcuatus* (Marques-Toigo) Archangelsky and Gamero, 1979 [Figure 5.3]

*Vallatisporites russoi* Archangelsky and Gamero, 1979

[Figure 5.4]

*Vallatisporites* sp. 1 [Figure 5.5]

*Vallatisporites* sp. 2 [Figure 5.6]

*Vallatisporites* sp. 3 [Figure 5.7]

*Cristatisporites inconstans* Archangelsky and Gamero, 1979 [Figure 5.10]



Suprasubturma Pseudosaccitritiletes Richardson, 1965  
 Infraturma Monopseudosacciti Smith and Butterworth, 1967  
*Spelaeotritiletes arenaceus* Neves and Owens, 1966 [Figure 5.9]  
*Spelaeotritiletes triangulus* Neves and Owens, 1966 [Figure 5.8]  
 Turma Monoletes Ibrahim, 1933  
 Suprasubturma Acavatomonoletes Dettmann, 1963  
 Subturma Azonomonoletes Lubert, 1935  
 Infraturma Laevigatomonoleti Dybová and Jachowicz, 1957  
*Laevigatosporites vulgaris* (Ibrahim) Ibrahim, 1933 [Figure 5.11]  
 Infraturma Sculptatomonoleti Dybová and Jachowicz, 1957  
*Striatosporites heyleri* (Doubinger) emend. Playford and Dino, 2000a [Figure 5.12]

#### Pollen grains

Anteturma Variegerminantes R. Potonié, 1970  
 Turma Saccites Erdtman, 1947  
 Subturma Monosaccites Chitaley emend. R. Potonié and Kremp, 1954  
 Infraturma Aletesacciti Leschik, 1955  
*Florinites occultus* Habib, 1966 [Figure 6.10]  
*Florinites* sp. [Figure 5.13]  
 Infraturma Vesiculomonoraditi Pant, 1954  
*Potoneisporites brasiliensis* (Nahuys, Alpern, and Ybert) emend. Archangelsky and Gamero, 1979 [Figure 6.5]  
*Potoneisporites densus* Maheshwari, 1967 [Figure 6.11]  
*Potoneisporites elegans* (Wilson and Kosanke) Wilson and Venkatachala emend. Habib, 1966 [Figure 6.3]  
*Potoneisporites neglectus* Potonié and Lele, 1961  
*Potoneisporites novicus* Bhargava, 1954 [Figure 6.2]  
*Potoneisporites ovatus* (Kar) Gutiérrez, 1993 [Figure 6.9]  
*Potoneisporites simplex* Wilson, 1962 [Figure 6.1]  
*Potoneisporites triangulatus* Tiwari, 1965 [Figure 6.8]  
*Potoneisporites* sp. [Figure 7.4]  
*Peppersites ellipticus* Ravn, 1979 [Figure 6.7]  
*Caheniasaccites ovatus* Bose and Kar emend. Gutiérrez, 1993  
*Costatascyclus crenatus* Felix and Burbridge emend. Urban, 1971 [Figure 6.4]  
 Infraturma Triletesacciti Leschik 1955  
*Cannanoropollis densus* (Lele) Bose and Maheshwari, 1968 [Figure 7.5]  
*Cannanoropollis korbaensis* (Bharadwaj and Tiwari) Foster, 1975 [Figure 6.6]  
*Plicatipollenites gondwanensis* (Balme and Hennelly) Lele, 1964 [Figure 7.6]

*Plicatipollenites trigonalis* Lele, 1964  
 Infraturma Striasacciti Bharadwaj, 1962  
*Striomonosaccites ovatus* Bharadwaj, 1962 [Figures 7.9, 9.1]  
*Meristocarpus explicatus* Playford and Dino, 2000 [Figure 8.6]  
 \**Meristocarpus ostentus* sp. nov. [Figure 7.1–7.3]  
 Subturma Disaccites Cookson, 1947  
 Infraturma Disaccitriteleti Leschik, 1955  
*Limitisporites* sp.  
 Infraturma Striatiti Pant, 1954  
*Illinites unicus* Kosanke, 1950 [Figure 7.7]  
*Protohaploxylinus amplus* (Balme and Hennelly) Hart, 1964 [Figure 8.4]  
*Protohaploxylinus bharadwajii* Foster, 1979 [Figures 7.8, 8.3]  
*Protohaploxylinus* sp. cf. *Striatopodocarpites magnificus* Bharadwaj and Saluja, 1964 [Figure 8.5]  
*Striatopodocarpites* sp. cf. *S. phaleratus* (Balme and Hennelly) Hart, 1964 [Figure 7.10]  
*Striatoabietes* sp. cf. *S. anaverrucosus* Archangelsky and Gamero, 1979 [Figure 8.7]  
*Taeniaesporites* sp. [Figure 8.8]  
 \**Lahiritites segmentatus* sp. nov. [Figures 8.1, 8.2, 9.2, 9.4]  
*Striatopodocarpites* sp. [Figure 8.9]  
 Turma Plicates Naumova emend. R. Potonié, 1960  
 Subturma Monocolpates Iversen and Troels-Smith, 1950  
*Cycadopites* sp.  
 Sculptured monocolpate form indet. [Figure 7.12]

#### Green algae (division Chlorophyta)

Class Chlorophyceae, order Chlorococcales  
*Botryococcus braunii* Kützing, 1849  
 Class Zygnemaphyceae  
*Brazilea scissa* (Balme and Hennelly) Foster, 1975 [Figure 7.11]

#### Systematic palaeontology

Genus *Brevitritiletes* Bharadwaj and Srivastava, 1969

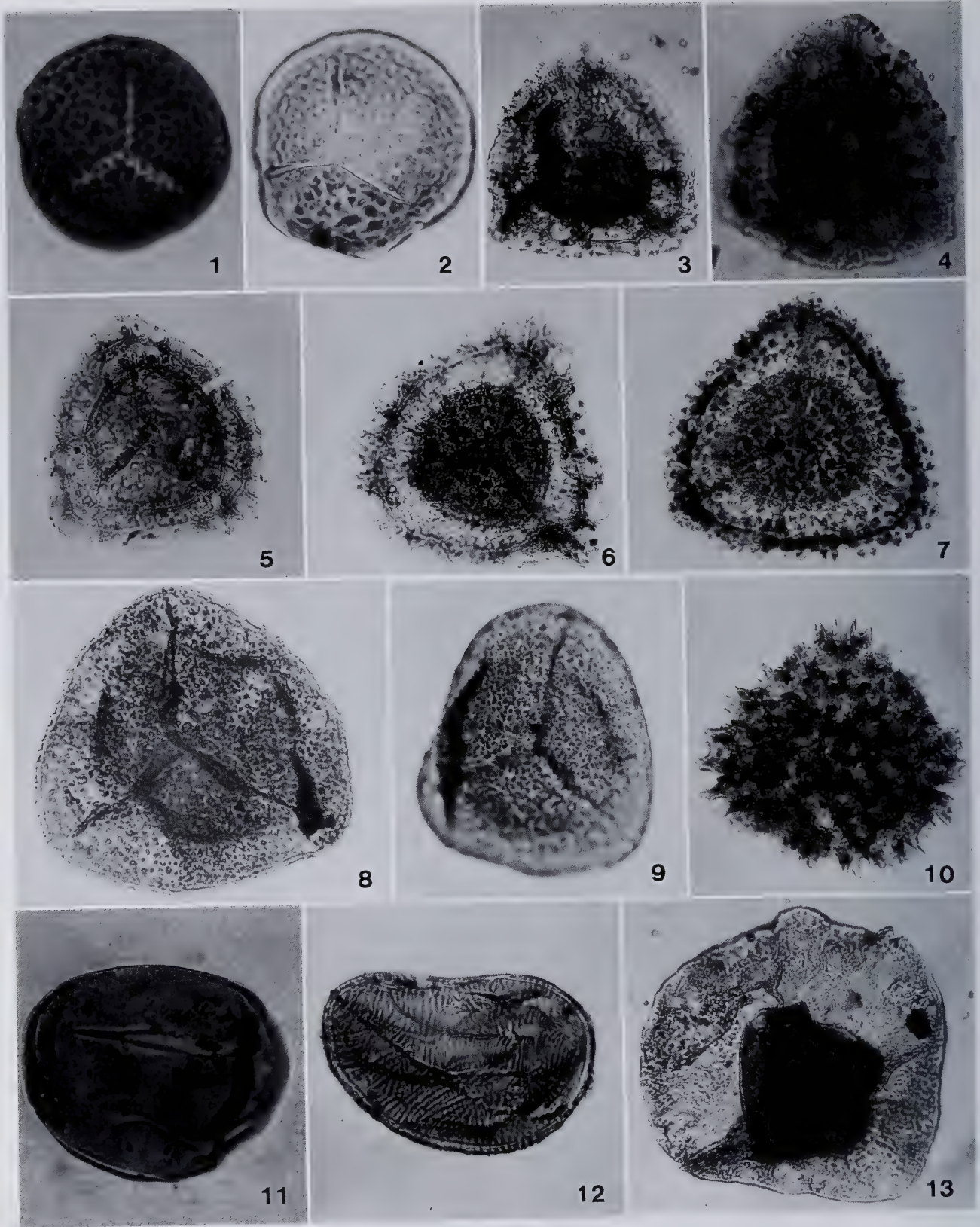
*Type species.*—*Brevitritiletes communis* Bharadwaj and Srivastava, 1969; by original designation.

*Brevitritiletes levis* (Balme and Hennelly)  
 Bharadwaj and Srivastava, 1969

Figure 3.9

*Apiculatisporites levis* Balme and Hennelly, 1956, p. 246–247, pl. 2, figs. 19–21.

*Brevitritiletes levis* (Balme and Hennelly) Bharadwaj and Srivastava, 1969, p. 226–227, pl. 1, figs. 17–20.





*Anapiculatisporites ? variornatus* Menéndez and Azcuy, 1969, p. 88, 90; pl. 3, figs. A–H.

*Apiculiretusispora variornata* (Menéndez and Azcuy) Menéndez and Azcuy, 1971, p. 28.

*Retusotriteles baculiferus* Ybert, 1975, p. 186, pl. 1, figs. 21–23. non *Apiculatisporis* [sic] *levis* Balme and Hennelly; Césari, Archangelsky, and Seoane, 1995, p. 78; pl. 1, fig. 2.

For further synonymy see Foster (1979, p. 35).

**Description.**—Spores radial, trilete. Amb circular, sub-circular, or very broadly rounded subtriangular. Laesurae distinct, straight, extending almost to equatorial periphery; simple or accompanied by narrow and somewhat irregular lips; frequently terminating in  $\pm$  distinct curvaturae imperfectae. Exine 1.5–2  $\mu$ m thick, sculptured distally and equatorially with small, discrete, apiculate elements comprising spinae, coni, and galeae, 1.2–2.5  $\mu$ m long (usually ca. 1.5–2  $\mu$ m), 0.5–2  $\mu$ m in basal diameter, spaced 0.5–2  $\mu$ m apart. Proximal surface laevigate or very sparsely and finely spinose/conate; sometimes polumbrate, with thickened (darkened) interradii emphasizing contact areas or parts thereof.

**Dimensions** (25 specimens).—Equatorial diameter, excluding sculptural projections, 22 (30) 37 m.

**Remarks and comparison.**—The specimens described above are in close accord with those described originally (Balme and Hennelly, 1956) and subsequently (Backhouse, 1991, 1993) from the Collie Coal Measures (Permian) of southwestern Australia, and also with Foster's (1979) material from Permian strata of the Bowen Basin, Queensland. In degraded specimens, the apiculate sculptural projections tend to exhibit decapitate or otherwise blunted termini and may thus resemble bacula. In terms of coarseness of sculpture, a morphological continuum exists among specimens belonging to *Brevitriteles levis* (Balme and Hennelly) Bharadwaj and Srivastava, 1969 (cf. Backhouse, 1991, p. 263).

Ybert's (1975) photomicrographs of his species *Retusotriteles baculiferus* leave no doubt as to its synonymy with *Brevitriteles levis*. The same is considered applicable to *Apiculiretusispora variornata* (Menéndez and Azcuy) Menéndez and Azcuy, 1971; see also Césari and Gutiérrez (2001, pl. 2, fig. 6). A specimen recorded by Césari *et al.* (1995, see above synonymy) as *Apiculatisporis* (sic) *levis* differs from the latter in having sparser, essentially rod-like sculpturing elements.

**Previous records.**—Known widely from the uppermost

Carboniferous and Permian of Gondwana. South American reports include those from Argentina (Menéndez and Azcuy, 1969, 1971; Mautino *et al.*, 1998; Vergel, 1998; Césari and Gutiérrez, 2001) and Brazil (Ybert, 1975; Burjack, 1978; Marques-Toigo, 1988).

Genus *Horriditriteles* Bharadwaj and Salujha, 1964

**Type species.**—*Horriditriteles curvibaculosus* Bharadwaj and Salujha, 1964; by original designation.

**Discussion.**—Foster (1979, p. 38) has clarified the diagnoses and differential diagnoses of *Horriditriteles* Bharadwaj and Salujha, 1964 and its type species.

*Horriditriteles uruguiensis* (Marques-Toigo)  
Archangelsky and Gamero, 1979

Figures 3.10, 4.3, 4.4

*Neoraistrickia uruguiensis* Marques-Toigo, 1974, p. 604, pl. 1, figs. 4, 5.

*Neoraistrickia baculicapillosa* Pons, 1976, p. 120–121, pl. 2, figs. 14–16.

*Horriditriteles uruguiensis* (Marques-Toigo) Archangelsky and Gamero, 1979, p. 424–426.

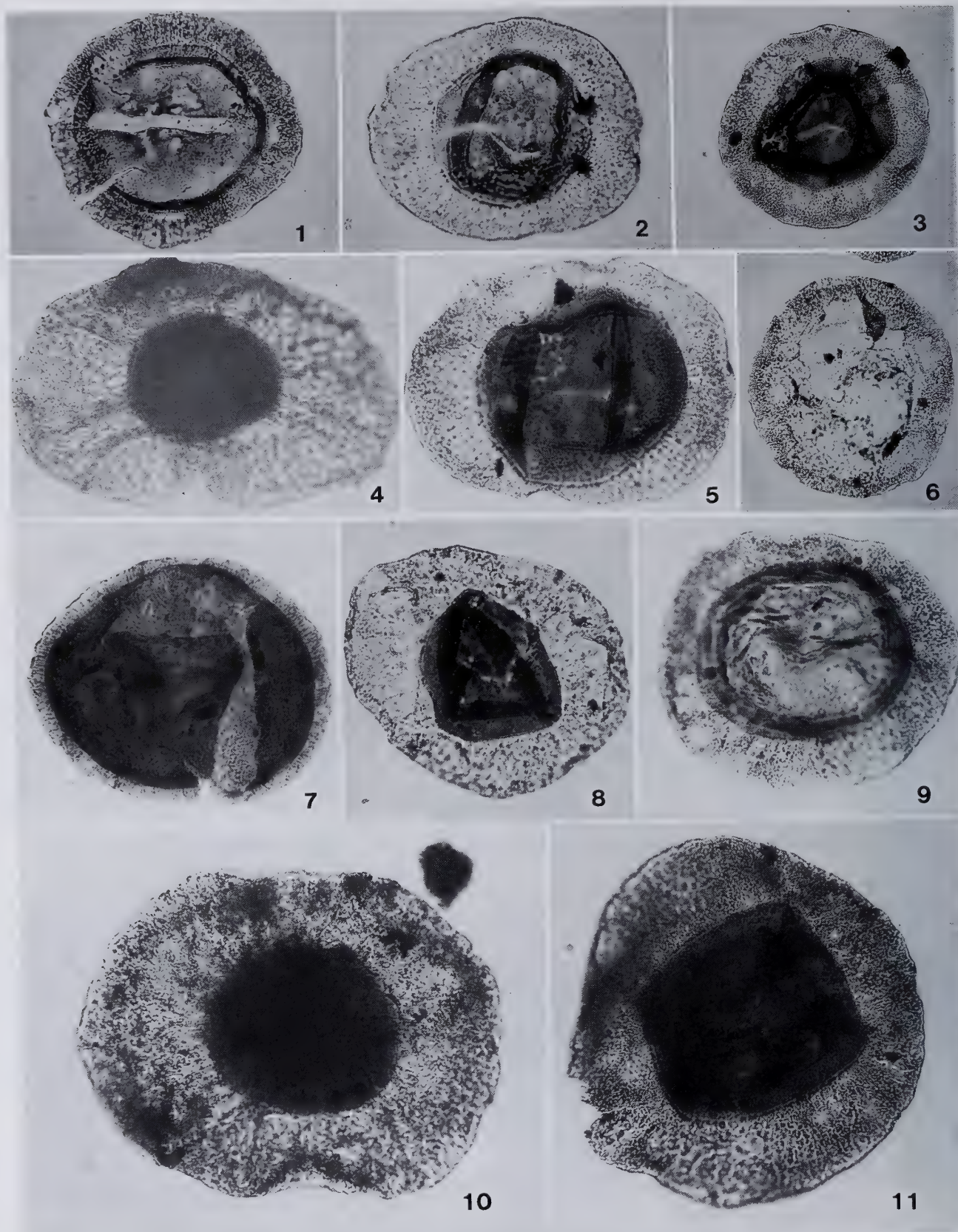
**Description.**—Spores radial, trilete. Amb subtriangular with straight or slightly concave sides and broadly rounded apices. Laesurae more or less distinct, straight, extending at least three-quarters of distance to equator, infrequently with narrow lip development. Exine 1–1.8  $\mu$ m thick, sculptured irregularly and heterogeneously with bacula (mainly), associated with verrucae, coni, spinae, and clavae of similar dimensions. Sculptural elements discrete and developed comprehensively, but more conspicuous distally and equatorially; length usually 1–4  $\mu$ m, bases 0.8–2.5  $\mu$ m in diameter and spaced 0.5–6  $\mu$ m apart.

**Dimensions** (20 specimens).—Equatorial diameter, excluding sculptural projections, 33 (43) 60  $\mu$ m.

**Comparison.**—*Horriditriteles uruguiensis* (Marques-Toigo) Archangelsky and Gamero, 1979 is distinguished from the type species (see Bharadwaj and Salujha, 1964, p. 193–194, pl. 2, figs. 34–39) by its larger size and more densely distributed sculpture; and from *H. ramosus* (Balme and Hennelly) Bharadwaj and Salujha, 1964, which has more uniformly baculate sculpture and subtriangular amb typically with slightly convex sides (Balme and Hennelly, 1956, p. 249, pl. 3, figs. 39–41).

◀ **Figure 5.** 1, 2. *Verrucosiporites andersonii*; 1,  $\times 750$ , 20005916/3, A49; 2,  $\times 750$ , 20005916/3, A47. 3. *Vallatisporites arcuatus*,  $\times 500$ , 20005916/3, D39. 4. *Vallatisporites russoi*,  $\times 750$ , 20005916/3, C54. 5. *Vallatisporites* sp. 1,  $\times 500$ , 20005916D, R39/3. 6. *Vallatisporites* sp. 2,  $\times 500$ , 20005916D, O36/4. 7. *Vallatisporites* sp. 3,  $\times 500$ , 20005916D, E50. 8. *Spelaeotriteles triangulus*,  $\times 750$ , 20005916D, F48/4. 9. *Spelaeotriteles arenaceus*,  $\times 750$ , 20005916D, O44. 10. *Cristatisporites inconstans*,  $\times 500$ , 20005916D, D48/4. 11. *Laevigatosporites vulgaris*,  $\times 750$ , 20005916E, H37/2. 12. *Striatosporites heyleri*,  $\times 500$ , 20005916D, S52. 13. *Florinites* sp.,  $\times 500$ , 20005916D, S57.







*Previous records.*—Originally described (Marques-Toigo, 1974) from the Lower Permian of Uruguay, *Horridites uruguaiensis* has been recorded subsequently in rocks of similar age from there and from Brazil and Argentina (e.g., Pons, 1976; Archangelsky and Gamero, 1979; Marques-Toigo, 1988; Beri and Goso, 1996; Dias, 1994; Césari *et al.*, 1995; Beri and Aguilar, 1998; Vergel, 1998). According to Césari and Gutiérrez (2001), this species occurs in the Upper Carboniferous-Lower Permian interval of central western Argentina.

Genus *Spelaeotriletes* Neves and Owens, 1966

*Type species.*—*Spelaeotriletes triangulus* Neves and Owens, 1966; by original designation.

*Discussion.*—Playford *et al.* (2001) have provided a comprehensive review of *Spelaeotriletes* Neves and Owens, 1966 in terms of its diagnosis, differential diagnosis, and Gondwanan representation.

*Spelaeotriletes* is represented commonly in the Piauí palynoflora by two species that were instituted concurrently by Neves and Owens (1966) and share very similar morphological attributes; viz., the type species *S. triangulus* (Figure 5.8) and *S. arenaceus* (Figure 5.9). Both species were described in detail by Playford and Dino (2000a, p. 21–22, pl. 5, figs. 1–7; pl. 6, figs. 5, 6) on the basis of numerous well-preserved specimens they encountered in the Pennsylvanian portion of the upper Palaeozoic Tapajós Group, Amazonas Basin. The difficulties that may arise in satisfactorily separating these species from each other have been discussed by Playford and Dino (2000a) and Playford *et al.* (2001); see also Spinner and Clayton (1973, p. 161), Playford and Powis (1979, p. 391), and Ravn and Fitzgerald (1982, p. 144). Pending re-examination of the respective type specimens of *S. triangulus* and *S. arenaceus*, and study of possible topotype material, the species are here distinguished – albeit somewhat provisionally as, for instance, in Playford *et al.* (2001) – in accordance with Neves and Owens's (1966, p. 345–346) original criteria (principally sculptural). These are that the exoexine (i.e., outside of the virtually laevigate contact faces) bears sculpturing elements that are generally coarser and more densely and regularly distributed in *S. triangulus* than in *S. arenaceus*.

*Previous records.*—*S. arenaceus* and *S. triangulus* have been reported widely, either individually or as a single merged specific entity, from upper Palaeozoic (more par-

ticularly, lower-middle Pennsylvanian) strata of both northern and southern hemispheres (Playford and Dino, 2000a, p. 21).

Genus *Meristocarpus* Playford and Dino, 2000b

*Type species.*—*Meristocarpus explicatus* Playford and Dino, 2000b; by original designation (monotypic).

*Meristocarpus ostentus* sp. nov.

Figure 7.1–7.3

*Meristocarpus* sp. C of Playford and Dino, 2000b, p. 100, pl. 4, figs. 1, 2.

*Diagnosis.*—Pollen grains bilateral, monosaccate, taeniate, monolete. Amb transversely oval to elongate, ends rounded. Laesura distinct to perceptible, straight or somewhat curved, length variable. Outline of corpus (in polar view) similar to amb, exine 1–1.5  $\mu\text{m}$  thick; proximal surface bearing 5–12 subparallel taeniae, mostly continuous, infrequently bifurcating, each 3–8  $\mu\text{m}$  wide, with intervening clefts 0.5–1.5  $\mu\text{m}$  wide. A pair of straight to broadly curved folds developed marginally across corpus and marking saccus attachments thereto. Saccus relatively narrow where adjoining transverse sides of corpus, with greatest development about longitudinal sides (“ends”) of corpus; fine to medium endoreticulum evident in well-preserved specimens.

*Dimensions* (19 specimens, in polar aspect).—Overall breadth 82 (92) 110  $\mu\text{m}$ ; overall length 34 (48) 65  $\mu\text{m}$ . Corpus breadth 55 (70) 82  $\mu\text{m}$ ; corpus length 27 (43) 60  $\mu\text{m}$ .

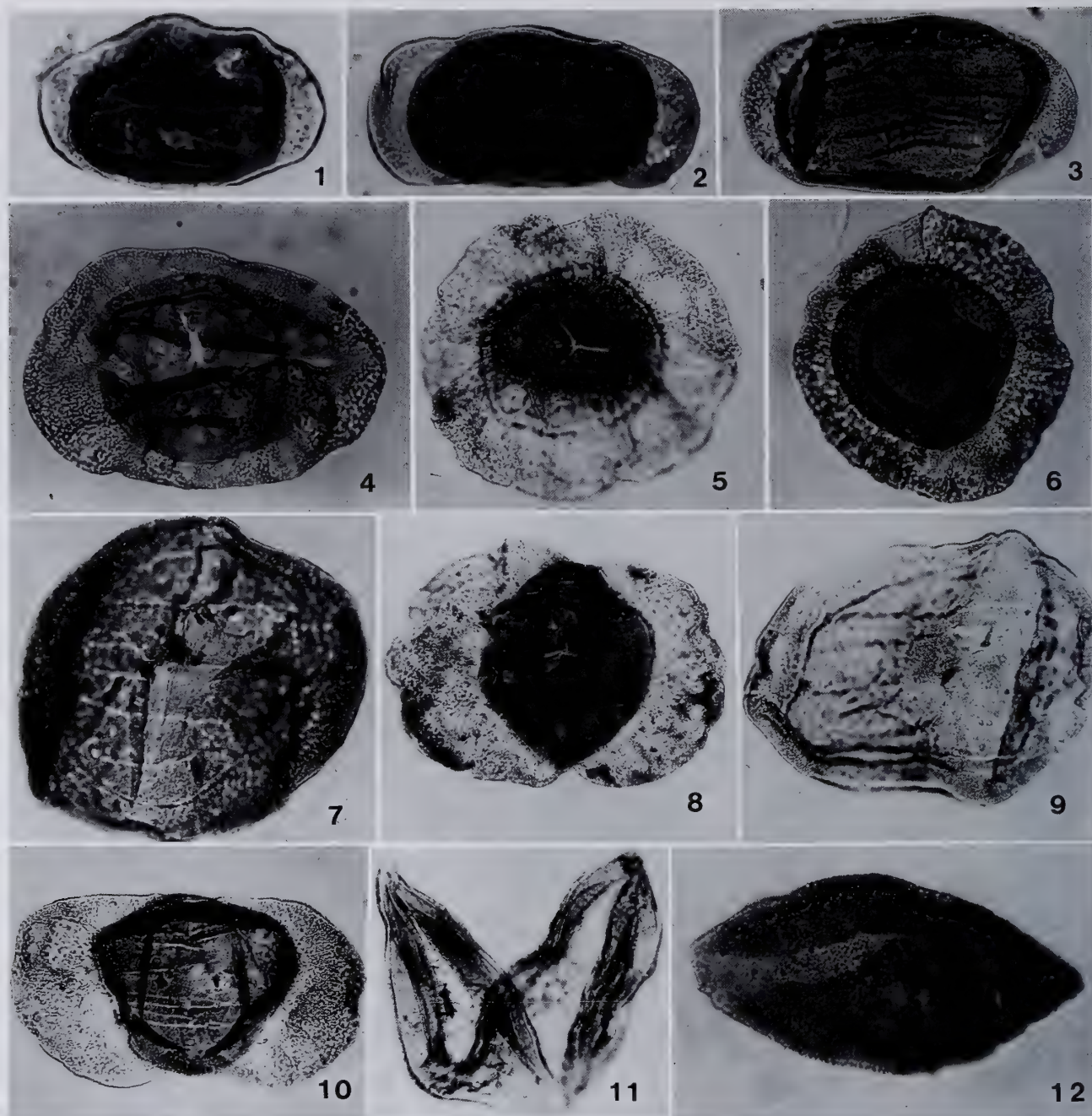
*Holotype.*—Slide 20005916/3, S38/1; Figure 7.3. Proximal aspect. Amb transversely elongate-oval; overall length 47  $\mu\text{m}$ , width 88  $\mu\text{m}$ ; corpus well-defined, 43  $\mu\text{m}$  long, 72  $\mu\text{m}$  wide, outline closely conforming with amb, proximal face modified by 7 subparallel transverse taeniae extending for full corpus breadth, some bifurcation but mainly continuity; longitudinal corpus margins with prominent, straight to outwardly convex folds; maximum sacchi development about corpus ends; sacchi with fine endoreticulation; laesura perceptible, slightly curved, length 13  $\mu\text{m}$ .

*Type locality.*—Brazil, Parnaíba Basin, Piauí Formation; 1-UN-23-PI well, core, 145.0 m.

*Etymology.*—From the Latin, *ostentus*, stretched out.

◀ **Figure 6.** 1. *Potonieisporites simplex*,  $\times 500$ , 20005916C, P34/1. 2. *Potonieisporites novicus*,  $\times 500$ , 20005916C, G34/4. 3. *Potonieisporites elegans*,  $\times 500$ , 20005916C, D44/3. 4. *Costatascyclus crenatus*,  $\times 500$ , 20005916/3, T57/3. 5. *Potonieisporites brasiliensis*,  $\times 750$ , 20005916A, M37/4. 6. *Cannanoripollis korbaensis*,  $\times 500$ , 20005916C, D39/4. 7. *Peppersites ellipticus*,  $\times 500$ , 20005916C, A39/2. 8. *Potonieisporites triangulatus*,  $\times 500$ , 20005916C, J41/2. 9. *Potonieisporites ovatus*,  $\times 500$ , 20005916B, T41/4. 10. *Florinites occultus*,  $\times 500$ , 20005916/2, U66. 11. *Potonieisporites densus*,  $\times 500$ , 20005916/3, C48/4.



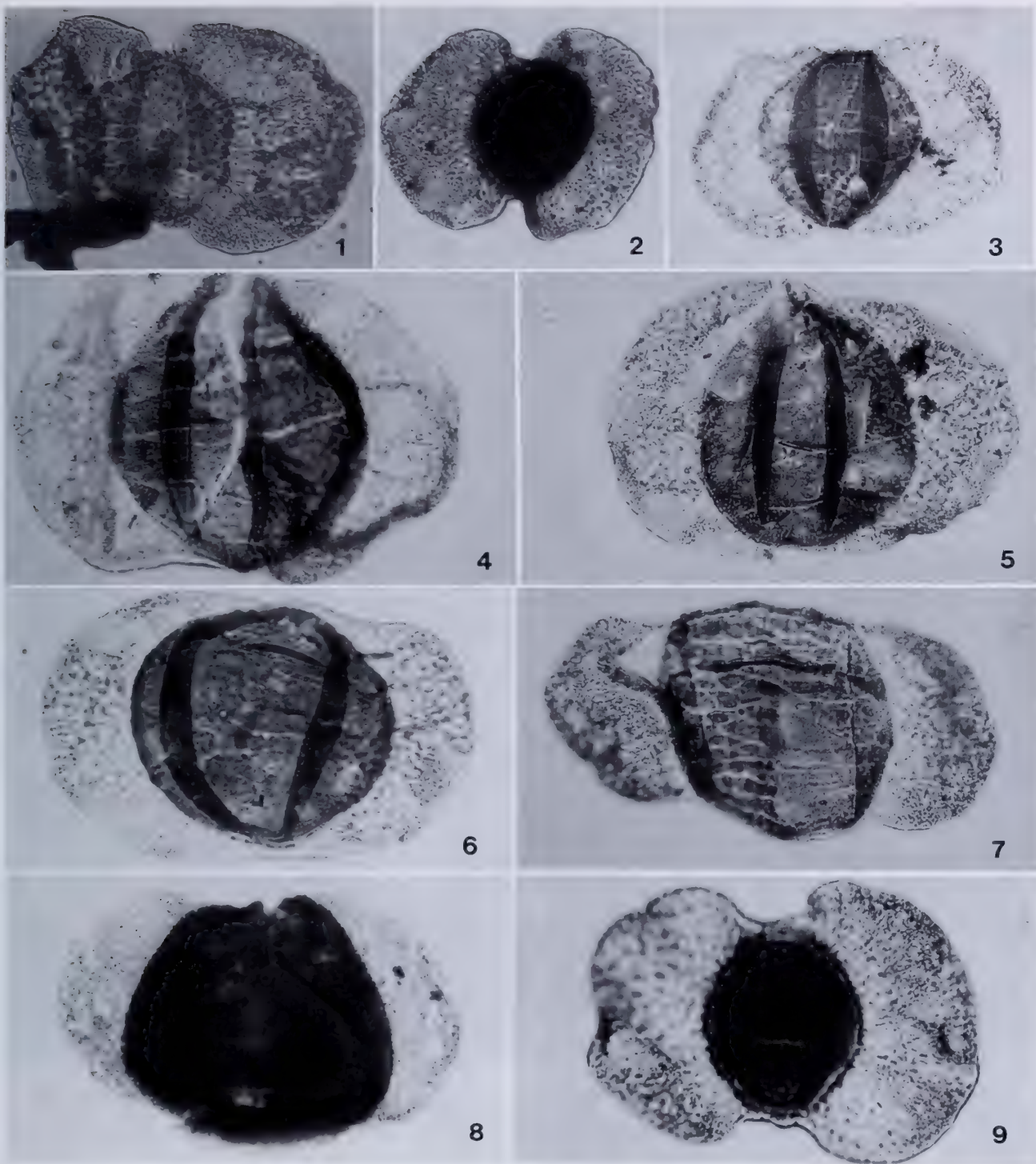


**Figure 7.** 1–3. *Meristocarpus ostentus* sp. nov.; 1,  $\times 750$ , 20005916/3, G50/3; 2,  $\times 500$ , 20005916B, O40/3; 3, holotype,  $\times 500$ , 20005916/3, S38/1. 4. *Potonieisporites* sp.,  $\times 500$ , 20005916D, G33/3. 5. *Cannanoropollis densus*,  $\times 500$ , 20005916D, M33. 6. *Plicatipollenites gondwanensis*,  $\times 500$ , 20005916F, P35/1. 7. *Illinites unicus*,  $\times 500$ , 20005916D,  $\times 50/3$ . 8. *Protohaploxylinus bharadwajii*,  $\times 500$ , 20005916/2, P57/3. 9. *Striomonosaccites ovatus*,  $\times 500$ , 20005916E, N/37. 10. *Striatopodocarpites* sp. cf. *S. phaleratus*,  $\times 500$ , 20005916C, F33/1. 11. *Brazilea scissa*,  $\times 750$ , 20005916/3, K46/2. 12. Sculptured monocolpate form indet.,  $\times 500$ , 20005916F, S44.

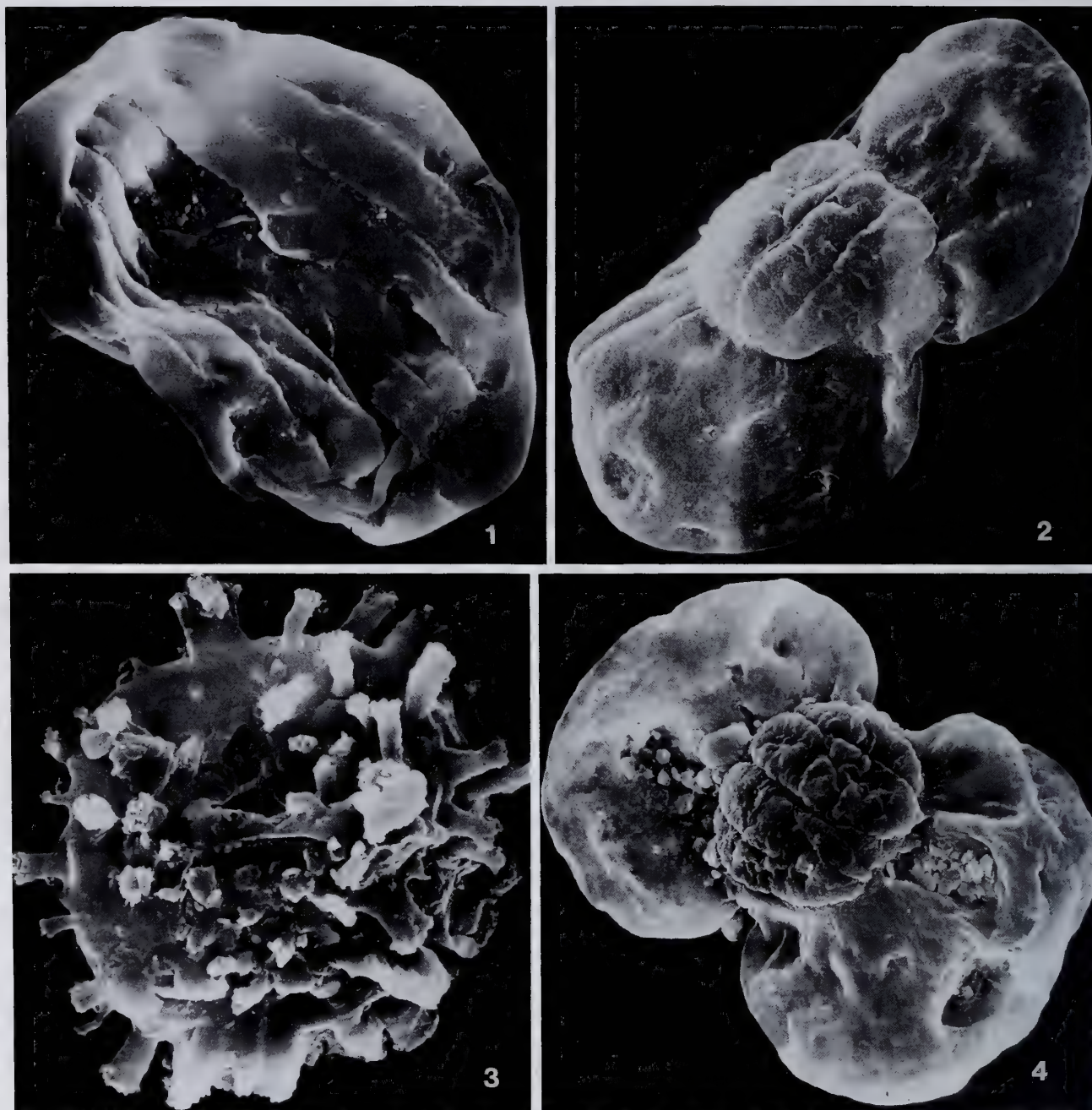
**Remarks.**—The identification herein of well-preserved specimens of this distinctive form, additional to those reported and designated informally by Playford and Dino

(2000b), enables its formal establishment as a new species. *Meristocarpus ostentus* sp. nov. is distinguished from other forms assigned to the genus mainly by the very prominent





**Figure 8.** 1, 2. *Lahirites segmentatus* sp. nov.; 1, holotype,  $\times 750$ , 20005916A, M58/2; 2,  $\times 500$ , 20005916A, E39. 3. *Protohaploxylinus bharadwajii*,  $\times 500$ , 20005916F, D48/1. 4. *Protohaploxylinus amplus*,  $\times 750$ , 20005916/3, C48/2. 5. *Protohaploxylinus* sp. cf. *Striatopodocarpites magnificus*,  $\times 500$ , 20005916C, A39/4. 6. *Meristocarpus explicatus*,  $\times 500$ , 20005916A, N39/3. 7. *Striatoabieites* sp. cf. *S. anaverrucosus*,  $\times 500$ , 20005916C, D35/3. 8. *Taeniaesporites* sp.,  $\times 500$ , 20005916C, D34/4. 9. *Striatopodocarpites* sp.,  $\times 500$ , 20005916/3, D41/4.



**Figure 9.** 1. *Striomonosaccites ovatus*,  $\times 1200$ , 20005916/S2, N39. 2, 4. *Lahirites segmentatus* sp. nov., 2,  $\times 800$ , 20005916/S2, N40/4; 4,  $\times 675$ , 20005916/S2, N55/4. 3. *Raistrickia cephalata*,  $\times 1500$ , 20005916/S2, P57/3.

elongation of its corpus and by relative proportions of the corpus and sacci.

*Previous records.* — From the Itaituba Formation, Amazonas Basin: *Illinites unicus* Zone, Westphalian C (Playford and Dino, 2000b).

#### Genus *Lahirites* Bharadwaj, 1962

*Type species.* — *Lahirites raniganjensis* Bharadwaj, 1962; by original designation (monotypic).

*Discussion.* — The salient attributes of *Lahirites* Bharadwaj, 1962, as exemplified by its type species, are circular



corpus bearing nine proximal transverse ("horizontal") taeniae that have a relatively coarse, segmented ("brickwork-like") appearance resulting from fine ("vertical"), linear, intra-taeniate channels cross-connecting the clefts bounding adjacent taeniae. The well-developed, protrusive sacci impart a distinctly diploxylonoid appearance. As discussed by Playford and Dino (2000b, p. 111), the three genera *Lahirites*, *Verticypollenites*, and *Hindipollenites*, as established by Bharadwaj (1962), have sufficient common features to render their mutual segregation problematical. Our choice of *Lahirites* as generic repository for the species newly described below is based mainly on its closer similarity to *L. raniganjensis* Bharadwaj, 1962 than to the type species of either of the other genera.

*Lahirites segmentatus* sp. nov.

Figures 8.1, 8.2, 9.2, 9.4

**Diagnosis.**—Pollen grains bisaccate, taeniate, strongly diploxylonoid. Corpus circular or near-circular with slight longitudinal elongation (polar orientation); exine 2–3  $\mu\text{m}$  thick, infragranulate. Cappa comprising 7–12 transverse taeniae that are continuous or, more commonly, irregularly furcant. Taeniae 7–10  $\mu\text{m}$  wide, separated by fine clefts 1–2  $\mu\text{m}$  wide; taeniae divided irregularly into broadly rectangular segments by fine channels disposed normally to inter-taeniate clefts, thus producing a brickwork-like negative reticulum. Cappula narrowly rectangular. Sacci > semicircular, with medium to coarse endoreticulum, distal attachment roots producing longitudinal folds near corpus borders.

**Dimensions** (16 specimens, in polar aspect).—Overall breadth 110 (135) 150  $\mu\text{m}$ ; overall length 63 (89) 105  $\mu\text{m}$ . Corpus breadth 35 (55) 65  $\mu\text{m}$ ; corpus length 50 (62) 75  $\mu\text{m}$ .

**Holotype.**—Slide 20005916A, M58/2; Figure 8.1. Proximal aspect. Strongly diploxylonoid; overall breadth 150  $\mu\text{m}$ , overall length 97  $\mu\text{m}$ ; corpus subcircular with slight longitudinal elongation (64  $\mu\text{m}$  x 75  $\mu\text{m}$ ), exine 2  $\mu\text{m}$  thick, featuring transverse, bifurcating taeniae, 7–10  $\mu\text{m}$  wide, separated by fine clefts and incised (approximately at right angles to the latter) by very narrow, irregular, and less distinct channels; cappula 23  $\mu\text{m}$  x 75  $\mu\text{m}$ ; sacci > semicircular, breadth 73  $\mu\text{m}$ , length 97  $\mu\text{m}$ , with medium-coarse endoreticulum.

**Type locality.**—Brazil, Parnaíba Basin, Piauí Formation; 1-UN-23-PI well, core, 145.0 m.

**Etymology.**—From the Latin, *segmentum*, partition, segment.

**Comparison.**—Certain Indian Permian species of *Lahirites* warrant comparison with *L. segmentatus* sp. nov. These species, with their principal morphological distinctions from *L. segmentatus*, are as follows: *L. raniganjensis*

Bharadwaj, 1962 (p. 92, pl. 13, fig. 172), taeniae non-furcant; *L. singularis* Bharadwaj and Salujha, 1964 (p. 204–205, pl. 8, figs. 119–121), generally smaller, corpus thin-walled but with distinct marginal ridge, non-furcant taeniae; and *L. rotundus* Bharadwaj and Salujha, 1964 (p. 205–206, pl. 8, fig. 125; pl. 9, figs. 126, 127), corpus with non-furcant taeniae and "laterally prominent marginal ridge".

### Correlation and age of palynoflora

Many of the palynomorphs in the present assemblage are identifiable with taxa that are known to have relatively broad stratigraphic ranges within the upper Palaeozoic of South America, and hence do not assist in definitive dating and correlation of the subject stratum. However, certain of the more vertically restricted species can usefully be applied biostratigraphically. These include the following: *Raistrickia cephalata*, *Vallatisporites arcuatus*, *Cristatisporites inconstans*, *Spelaotriletes arenaceus*, *S. triangulus*, *Striatosporites heyleri*, *Peppersites ellipticus*, *Illinites unicus*, and *Meristocarpus explicatus*. All have been documented previously from the upper Palaeozoic of Brazil (Amazonas Basin principally: Playford and Dino, 2000a, b) and/or of Argentina (e.g., Archangelsky and Gamero, 1979, Archangelsky *et al.*, 1996, Césari and Gutiérrez, 2001).

Müller's (1962) palynostratigraphic study included analysis of the Piauí Formation as cored in 15 oil exploration wells in the Parnaíba Basin (then termed Maranhão Basin). He recognized, in descending order, zones K, L, and M, covering the Piauí and the overlying Pedro de Fogo Formation and, supposedly (and, we believe, mistakenly), part of the underlying Poti Formation. The zones cannot be regarded, on present standards, as rigorously defined biostratigraphic units; they were ascribed generally to the Pennsylvanian (Westphalian-Stephanian). Zones L-M, represented by the Piauí Formation, include some forms encountered in the present sample; i.e., *Cristatisporites inconstans* (Müller's "Tl-2-I"), *Vallatisporites arcuatus* ("Tl-2-e"); *Verrucosisporites* sp. cf. *morulatus* ("Tl-r-b"), *Raistrickia cephalata* ("Raistr-a"), *Protophaploxylinus bharadwajii* ("V-D-i/st-a1"), and possibly *Spelaotriletes* sp. ("Tl-z-b"). Accordingly, the sample studied here is compatible with zones L-M (more particularly, the latter) of Müller (1962).

With regard to the Amazonas Basin, no really precise equivalence of the present assemblage can be established vis-à-vis the Playford and Dino (2000b) palynozonation of the upper Palaeozoic Tapajós Group. This may well be a consequence of the current study being based on only one, fortuitously productive sample from within an otherwise non-palyniferous Piauí interval. Moreover, very little is



known of the Parnaíba Basin's overall Carboniferous-Permian palynological sequence. Species considered to be stratigraphically significant in the Tapajós Group, and occurring also in the Piauí sample, include *Illinites unicus*, *Striatosporites heyleri*, and *Raistrickia cephalata*. Prima facie, therefore, the Piauí assemblage could be regarded as falling somewhere within the Amazonas zonal interval defined eponymously and collectively by these three species. However, viewed in more detail, it should be noted that both *S. heyleri* and *R. cephalata* are represented very sparingly, by only one or two specimens, in contrast to their respective zonal abundances in the Amazonas Basin. Correlation with the *Illinites unicus* Zone (Playford and Dino, 2000b, p. 120–121) appears most likely from the presence of *I. unicus* in association with *Meristocarpus explicatus* and *M. ostentus* and with plentiful *Spelaotriletes triangulus*, *S. arenaceus*, and zonate-cingulizionate forms (*Vallatisporites*, *Cristatisporites*). Additional support for this zonal correlation is provided by the scant representation of taeniate bisaccate pollen grains (which become increasing prevalent in post-*I. unicus* palynozones).

The *Illinites unicus* Zone embraces the upper part of the Itaituba Formation, directly beneath the Nova Olinda Formation, in the Tapajós Group succession of the Amazonas Basin. Hence, zonal attribution of the study sample signifies correlation of at least the subject Piauí stratum with the upper Itaituba Formation. This effectively corroborates other palaeontological evidence (previously cited herein) of faunal affinities between the Itaituba and Piauí Formations, and strengthens the lithostratigraphic correlation between these two formations that was originally advanced by Mesner and Wooldridge (1964). It follows that the upper part of the lower Piauí Formation can be ascribed a mid Pennsylvanian (late Westphalian) age (Playford and Dino, 2000b, p. 131).

Correlation of the present Piauí sample with the Argentinian palynozonation cannot be effected in any satisfactory way owing to the very generalized characteristics promulgated for those zones (Césari and Gutiérrez, 2001, p. 133). The best that can be said is that the Piauí suite would be attributable to the zones DMb or DMc.

#### Palaeoenvironmental inferences

As discussed previously, sedimentological and palaeontological studies indicate an interplay of several environmental circumstances or settings nonmarine, paralic, marine, evaporitic during accumulation of the Piauí Formation. Many lines of evidence, including data from core descriptions, well logs, remote sensing, lithofacies analyses, and sedimentary petrography, point to the lower part of the formation being predominantly nonmarine and reflecting

conditions of aridity.

In the studied sample, the abundant land-derived plant debris in association with wholly terrestrial palynomorphs surely attest to nonmarine conditions. Moreover, the prevalence of monosaccate pollen grains, produced by cordaitalean gymnosperms, suggest arid climatic conditions. Regarding the green algal palynomorphs, the presence of *Botryococcus* permits no unequivocal palaeoenvironmental inferences (e.g., Batten and Grenfell, 1996, p. 210), other than indicating a quiescent aquatic situation; but *Brazilea* is suggestive of an exclusively freshwater habitat (Colbath and Grenfell, 1995).

#### Conclusions

1. The spore-pollen palynoflora recovered from the single productive sample, representing the upper part of the lower Piauí Formation in the southern Parnaíba Basin, comprises pteridophytic trilete spores associated with a range of gymnospermous pollen grains, principally monosaccates. Taeniate bisaccates are relatively uncommon.

2. In biostratigraphic terms, the assemblage bears closest similarity to the *Illinites unicus* palynozone of the Tapajós succession in the Amazonas Basin.

3. The zonal attribution connotes correlation of the palyniferous Piauí stratum with the upper part of the Itaituba Formation of the Tapajós Group, and dating of the stratum as mid Pennsylvanian (late Westphalian).

4. Such palaeoenvironmental indications that can be gleaned from the palynoflora corroborate the sedimentological, geophysical, and other prior data that imply a nonmarine depositional situation under arid conditions.

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# Indian metoposaurid amphibians revised

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**Abstract.** A recent collection of more than a hundred fossil bones belonging to at least six individuals of metoposaurids from the basal part of the Late Triassic, Maleri Formation of the Pranhita-Godavari valley, Gondwana succession, has helped to formulate new ideas. Detailed morphological studies have been used to include all specimens of metoposaurids so far collected from India within a single taxon, *Buettneria maleriensis*, a new combination. A reconstruction of the skeleton of *Buettneria maleriensis* is presented for the first time. *Buettneria maleriensis* remains are common in the continental red beds of India, deposited under fluvial conditions witnessing seasonal climate changes. While some bones of *Buettneria maleriensis* were rolled and transported after death and are now found as sporadic fossils in mudstone (or occasionally in sandstones and calcirudites), the other type of occurrences, the rich accumulation of bones, are present only in mudstones. *Buettneria maleriensis* was replaced by the Chigutisauridae, a temnospondyl family exclusive to Gondwanaland. India is the only place where both metoposaurids and chigutisaurids are found in such close succession. The paleoposition of India during the later part of the Triassic may have been responsible for this.

**Key words:** *Buettneria*, India, Late Triassic, Maleri Formation

## Introduction

The Metoposauridae is a Late Triassic temnospondyl amphibian family known from Europe, North America, North Africa and India. They were quite large (at least 1.5 m in length), essentially aquatic animals (Defauw, 1989), with flat and heavily ornamented skull roofs marked with lateral line canals. Metoposaurids are to some extent morphologically similar to the present day crocodiles. However, unlike crocodiles, they had limbs unsuitable for quick movement on land.

The first metoposaurid, *Metoposaurus diagnosticus* (Meyer, 1842), was described from Europe. Subsequently a large number of metoposaurids belonging to several genera and species have also been reported from Europe and North America (Fraas, 1889, 1896, 1913; Lydekker, 1890; Watson, 1919; Romer, 1947; Colbert and Imbrie, 1956 and Werneburg, 1990). Dutuit (1976) carried out a study of another population of metoposaurids from North Africa. The Metoposauridae as a whole was extensively revised by Hunt (1993). However, Indian metoposaurids have not been studied in similar detail. Lydekker (1885) and Huene (1940) were the early workers to report metoposaurid fragments from India and Colbert (1958) discussed the significance of Indian metoposaurids in some detail. Later, Roychowdhury (1965) studied the Indian metoposaurids and recently a partial skull was described by Sengupta (1992).

A revision of the Indian metoposaurids has been attempted here in the light of the recovery of more than a hundred fossilised bones belonging to at least six individuals. These remains represent a mass accumulation and were found near Aigerapalli village in the basal part of the Maleri Formation of the Pranhita-Godavari valley of Central India.

Taphonomic and palaeobiogeographic studies of the metoposaurids have also revealed some interesting results. India is the only region where the typically Laurasian metoposaurs are found together with some stereospondyls exclusive to Gondwanaland. The significance of this association will be discussed.

## Family Metoposauridae

The family Metoposauridae is morphologically a very compact group which shares a number of character states. They have flat elongate skulls with tapering snouts, dorsolateral and anteriorly placed orbits, a pineal foramen far posterior to the orbits, low skulls with occipital condyles placed in the same line and plane (or a little posterior in certain cases) as the quadrate condyles, large paraquadrate foramina, spoollike intercentra (Romer, 1947; Watson, 1919, 1962; Colbert and Imbrie, 1956; Rouchowdhury, 1965; Dutuit, 1976) and wide cultriform process of the parasphenoid (Coldiron, 1978). In addition, Milner

(1990) noted that the palatine ramus of the pterygoid is rather short with a posteromedial ramus of the ectopterygoid contributing to the strut. Jupp and Warren (1986) stated that, in metoposaurids, the posterior coronoid forms part of the dorsal margin of the posterior Meckelian foramen. Warren and Snell (1991) further noted that the ilium of the metoposaurids has some taxonomic importance since the iliac blade is not "expanded" like other temnospondyls. They also noted that the metoposaurid humerus has well developed ends and prominent areas for muscle insertion, a rare trait among the temnospondyls. Both Werneburg (1990) and Warren and Snell (1991) suggested that the interclavicles of the metoposaurids have some characteristic features.

While the monophyly of the family Metoposauridae is established, the taxonomy at the generic level is somewhat problematic. There are only a few character states which are variable between different populations as well as within the single population of a particular area. The problem of taxonomy of metoposaurids at the generic level thus depends on proper understanding of those limited numbers of character states.

Colbert and Imbrie (1956) used two character states to differentiate the North American from the European populations. In the North American populations the lachrymal enters the orbit margin while in the European forms it does not. The degree of overlap of the clavicles on the interclavicles and the pattern of ornamentation of the clavicles were also different in the North American and European metoposaurids.

Roychowdhury (1965) grouped all the metoposaurid genera into a single genus, *Metoposaurus*. Subsequently Dutuit (1976) erected some new species from North Africa and designated them as *Metoposaurus* at the generic level. Gregory (1980) pointed out that there are at least two metoposaurid genera present in North America; one with an otic notch and the other without. Davidow-Henry (1989) divided the metoposaurids into three generic groups, one with otic notches, one without, and a third having a pineal foramen placed more forward than in the others. This splitting was continued by the recent work on metoposaurid taxonomy by Hunt (1993) and Milner (1994). Hunt (1993) divided the metoposaurids into five genera and six species. They are: *Metoposaurus diagnosticus* (Meyer, 1842), *M. bakeri* (Case, 1931), *Buettneria perfecta* (Case, 1922), *Dutuitosaurus ouazzoui* (Dutuit, 1976, new combination *sensu* Hunt, 1973), *Arganasaurus lyazidi* (Dutuit, 1976, new combination *sensu* Hunt, 1973) and *Apachesaurus gregorii* (Hunt, 1993). Hunt stated that the last-mentioned genus has a very shallow otic notch while in the other genera they are deeper.

The most conspicuous change in the work of Hunt (1993) is the lumping of many taxa found from various

places of the world into *Buettneria perfecta*, which also includes the Indian metoposaurid, *Metoposaurus maleriensis* (Roychowdhury, 1965), making it a junior synonym of *B. perfecta*. All the species of *Buettneria* have their lachrymals included within the border of the orbits.

Following a different approach, Milner (1994) grouped the metoposaurids into more than one "grade" which are further divided into certain "clades." He included "*M. maleriensis*" within the clade *Anaschisma*. The latter according to him is a "terminal clade" with the elongate lachrymal entering the orbit margin (a character-state of grade *Buettneria*), large, closely spaced nares and the supraorbital lateral line canals always broken behind the orbits (character states which separate *Anaschisma* from *Buettneria*).

### Indian metoposaurids

The history of the work on Indian metoposaurids was discussed in detail by Roychowdhury (1965). Only one more specimen of the family has been described in recent years by Sengupta (1992). Hence only a brief discussion on the Indian metoposaurids is provided below.

In India metoposaurids are known from the Maleri Formation of the Pranhita Godavari (P-G) valley and the Tiki Formation of the Son Mahanadi valley. Initially, the Indian metoposaurids were known from fragmentary surface collections which did not permit diagnosis below family level (Lydekker, 1885; Huene, 1940). Later, systematic collection of *in situ* specimens from the Maleri Formation yielded a number of well preserved fragments. These fragments were sufficiently diagnostic and included at least two partial skulls, clavicles and interclavicles, and vertebral elements. Roychowdhury (1965) erected *Metoposaurus maleriensis* on the basis of these specimens and also presented a restoration of the skull.

As mentioned earlier Hunt (1993) included *M. maleriensis* as *Buettneria perfecta*. The taxonomic status of the Indian metoposaurids is revised in the present work. All the specimens of the Indian metoposaurids are grouped into a single genus and species, *Buettneria maleriensis*, a new combination.

### Systematic paleontology

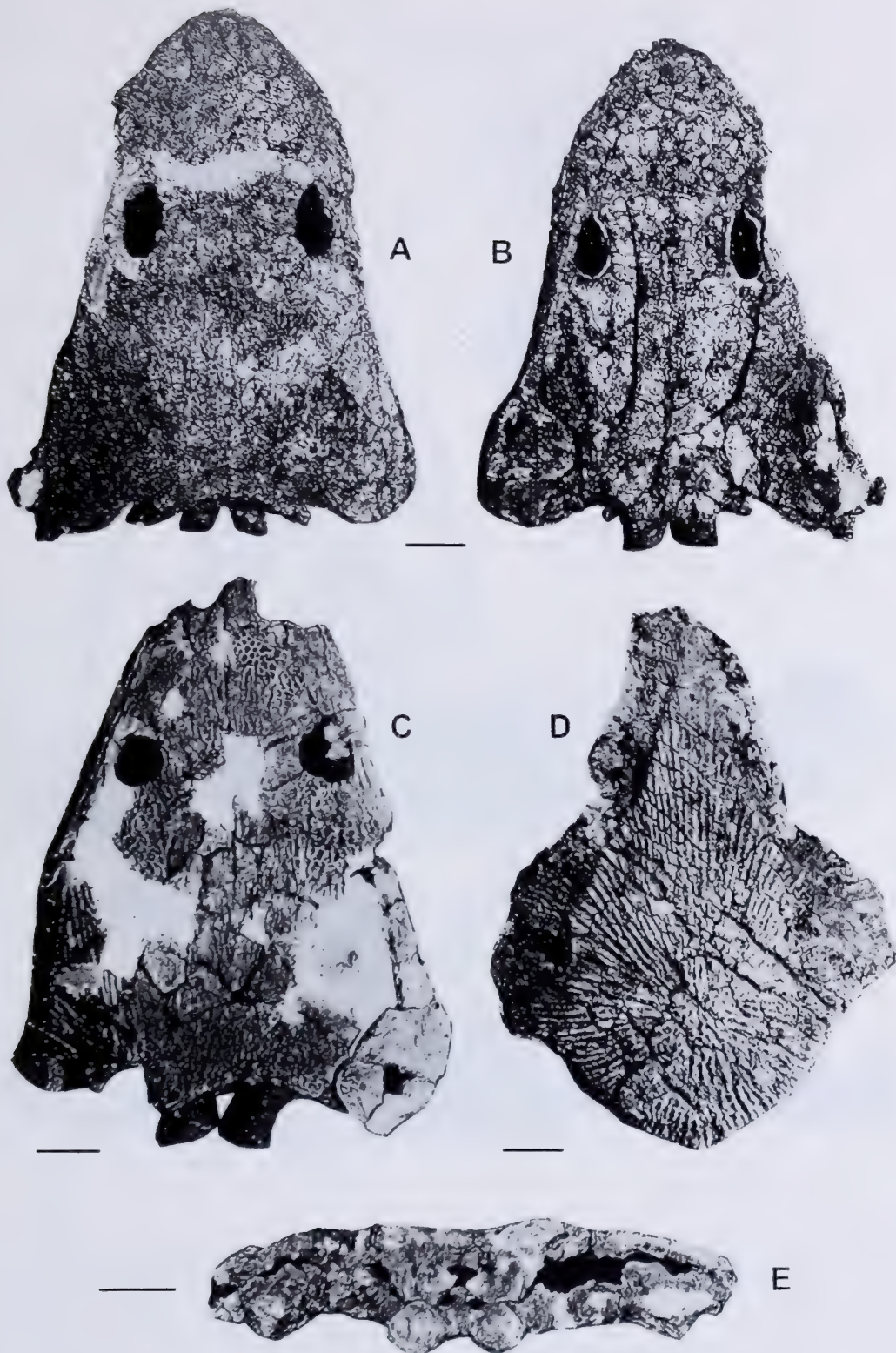
Order Temnospondyli Zittel, 1888  
Family Metoposauridae Watson, 1919  
Genus *Buettneria* Case, 1922

*Buettneria maleriensis* (Roychowdhury, 1965)  
new combination

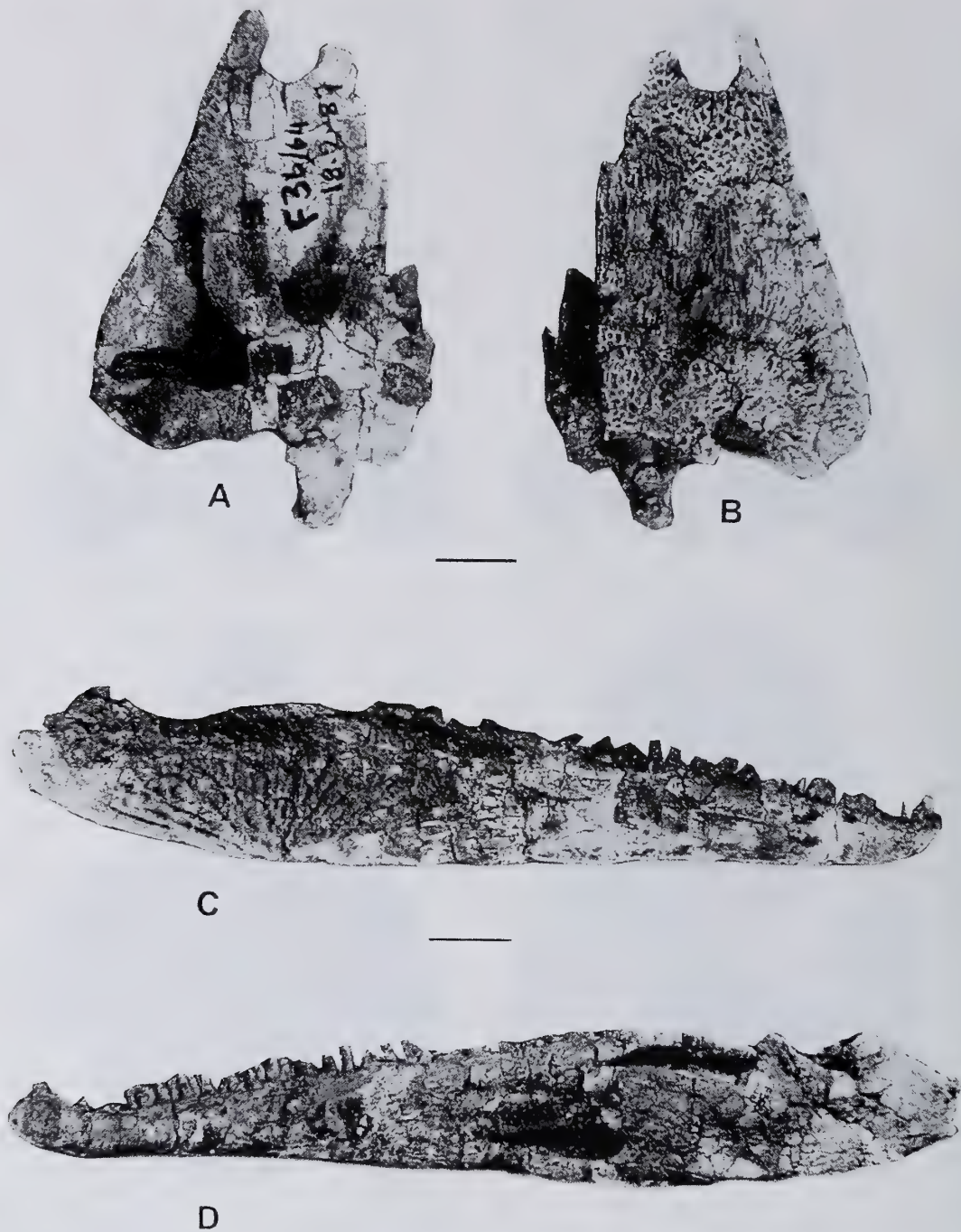
Figures 1-16

*Metoposaurus maleriensis* Roychowdhury, 1965, p. 21, figs. 3-



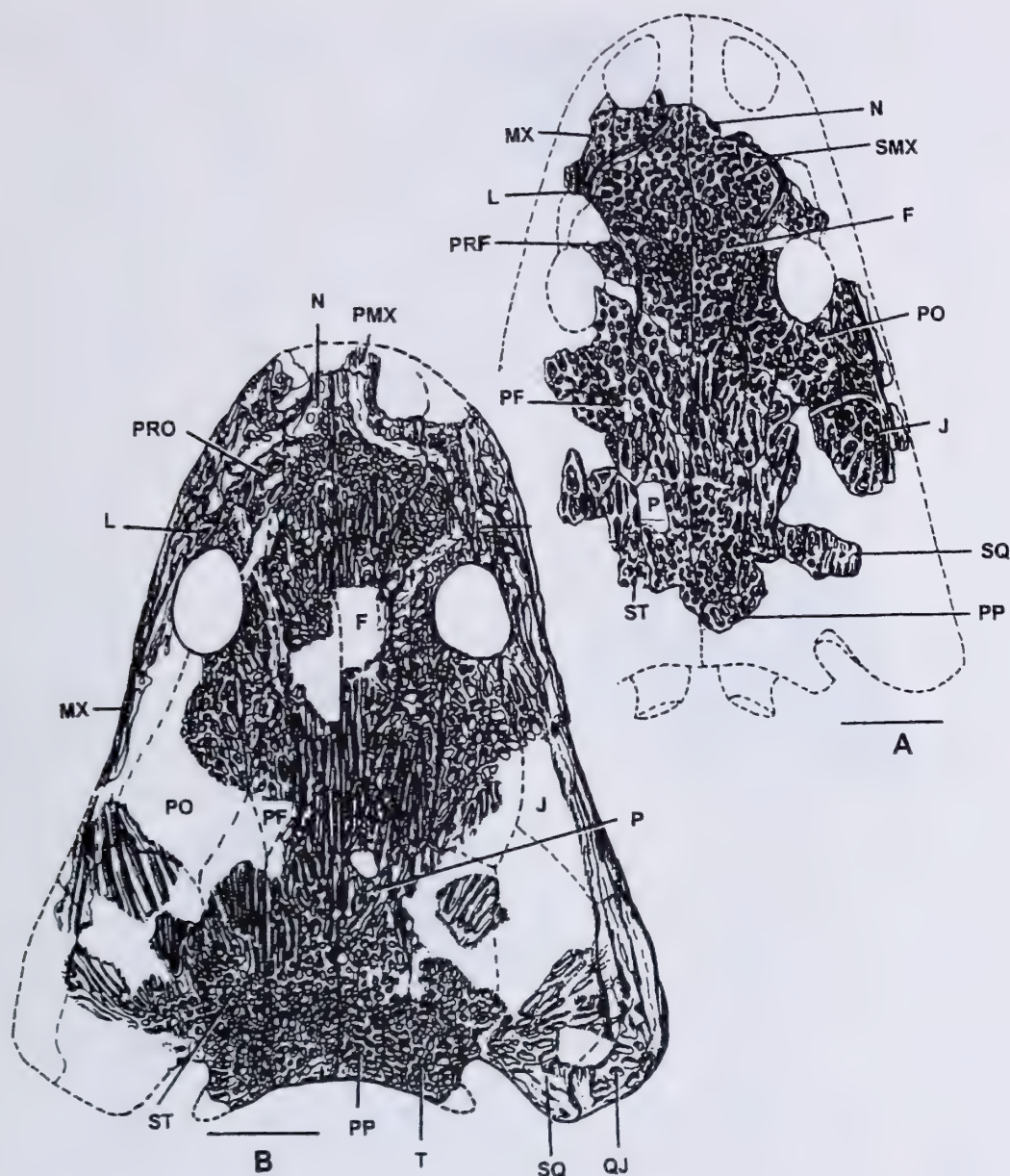


**Figure 1.** Skull roof (A = ISIA 56, C = ISIA 59), palate (B = ISIA 56), interclavicle (D = ISIA 67) and occiput (E = ISIA 53) of *Buettneria maleriensis*, new combination. Scale bars = 5 cm.



**Figure 2.** Palate (A = ISIA 58), skull roof (B = ISIA 58) and mandible (C, D = labial and lingual view of ISIA 60) of *Buettneria maleriensis*, new combination. Scale bars = 5cm.





**Figure 3.** Skull roof of *Buettneria maleriensis*, new combination. A = ISI A 4, B = ISI A 59. Abbreviations: F = frontal; J = jugal; L = lacrimal; N = nasal; P = parietal; PRF = prefrontal; PMX = premaxilla; PO = postorbital; PP = postparietal; PF = postfrontal; QJ = quadratojugal; SQ = squamosal; ST = supratemporal; T = tabular. Scale bars = 5 cm.

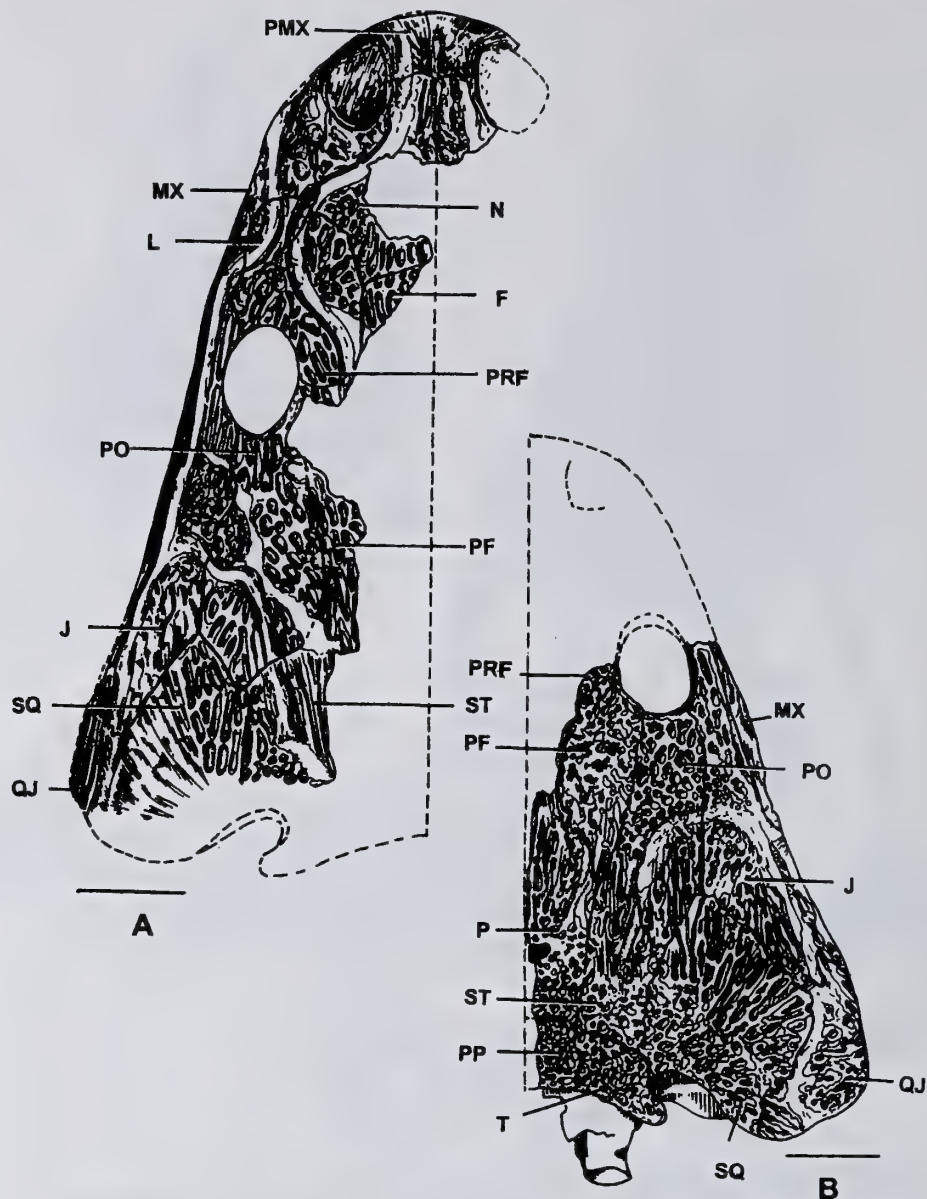
20, pls. 21–41; Sengupta, 1992, p. 300, figs. 1–4, pl. 1. *Buettneria perfecta*, Hunt, 1993, p. 78, figs. 7–9 (in part).

**Material examined.**—GSI 2249, 2254 and 2263 (Lydekker, 1885), K 33/638, 616a, b, 630a, 606a, 611a, 602a (Huene, 1940), ISI A 1 to 17 (Roychowdhury, 1965), ISI A 53 (Sengupta, 1992), ISI A 56, and ISI A 58 to 175. The specimens with numbers starting with ISI A are housed in the Geological Museum, Indian Statistical Institute, Calcutta, India (Table 1) and specimens K 33/638, 616a, b, 630a, 606a, 611a, 602a, and GSI 2249, 2254 and 2263 are kept in the Indian Museum, Calcutta, India.

**Holotype.**—ISI A 4, in the collection of the Geology Museum, Indian Statistical Institute, Calcutta, India.

**Paratypes.**—ISI A 1 to 3 and ISI A 5 to 17, 53, 56, 58 to 175.

**Distribution and age.**—*B. maleriensis* occur in the lower part of the Maleri Formation of the Pranhita Godavari val-



**Figure 4.** Skull roof of *Buettneria maleriensis*, new combination, **A** = ISI A 8, **B** = ISI A 58. Abbreviations used are same as Figure 3. Scale bars = 5 cm.

ley and also in the Tiki Formation of the Son Mahanadi valley of Central India. Material examined were mostly collected around the villages of Achlapur, Gampalpalli and Aiegarapalli, Adilabad District of Andhra Pradesh, India. The age of *B. maleriensis* is Late Carnian.

**Diagnostic characters.**—*Buettneria maleriensis* has the lachrymal in the margin of the orbits and thus it differs from all other metoposaurids except *B. perfecta*, *sensu* Hunt (1993). *B. maleriensis* differs from most specimens of *B. perfecta* in the presence of large, closely spaced nares and lateral line canals never forming a loop behind the or-

bits (Milner, 1994). Two specimens (FMNH UC 447 and 448, kept in the Field Museum of Natural History, University College collection, Chicago) designated as "*Anaschisma*" by Branson, 1905 have similarity with *B. maleriensis* in this regard. *B. maleriensis*, however, has a different type of ornament than that of "*Anaschisma*" and has a comparatively larger orbit.

The lachrymal is present as a narrow strip of bone in *B. maleriensis*. The anterior boundary of the lachrymal and that of the prefrontal are at the same level. All the specimens of *B. maleriensis* are unique in having parts of the



**Table 1.** List of the specimens of *Buettneria maleriensis*, new combination, housed in the Geology Museum, Geological Studies Unit, Indian Statistical Institute (ISI) Calcutta.

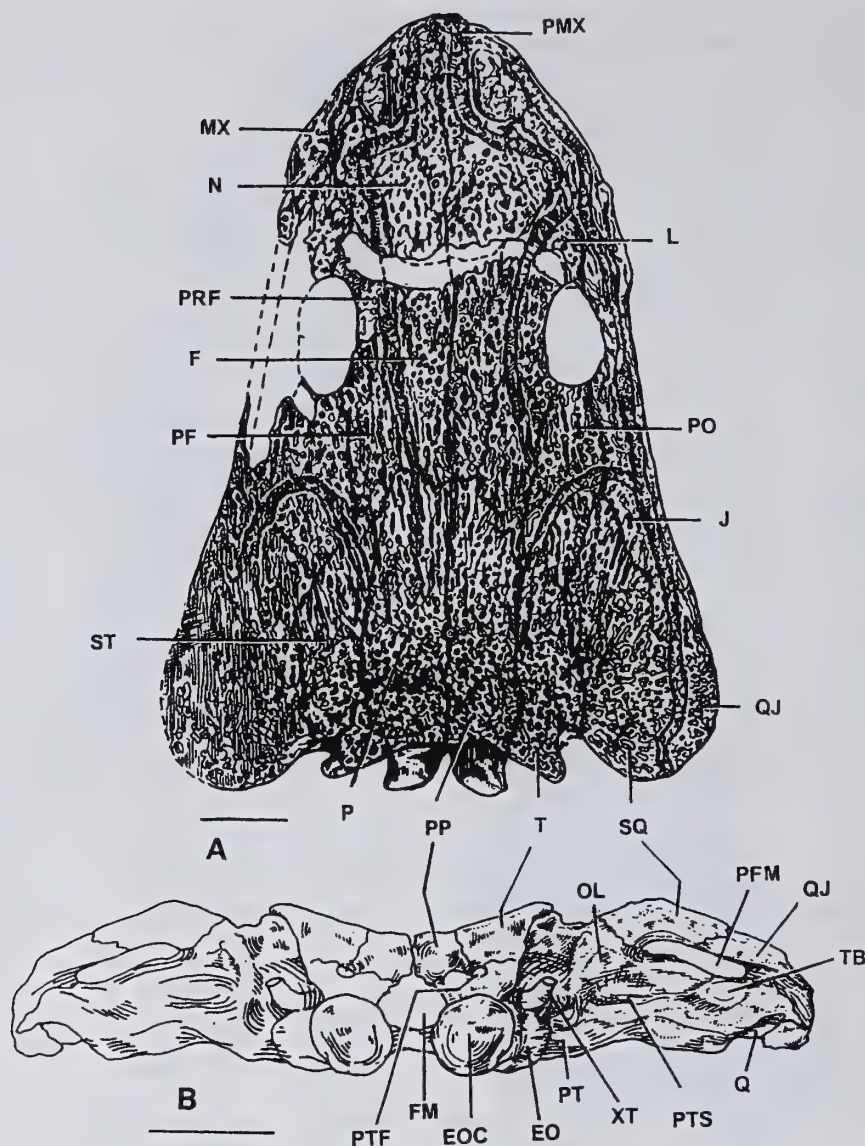
Element	ISI no.	Element	ISI no.	Element	ISI no.
Part of skull	ISI A 1	Femur, Right	ISI A 84	Intercentrum (Dorsal)	ISI A 129
Part of skull	ISI A 2	Femur, Right	ISI A 85	Intercentrum (Dorsal)	ISI A 130
Part of skull	ISI A 3	Ilium, Right	ISI A 86	Intercentrum (Dorsal)	ISI A 131
Part of skull	ISI A 4	Ilium, Right	ISI A 87	Intercentrum (Dorsal)	ISI A 132
Left squamosal	ISI A 5	Ilium, Right	ISI A 88	Intercentrum (Dorsal)	ISI A 133
Part of skull	ISI A 6	Scapulacoracoid, Rt	ISI A 89	Atlas	ISI A 134
Part of skull	ISI A 7	Scapulacoracoid, Rt	ISI A 90	Atlas	ISI A 135
Part of skull	ISI A 8	Scapulacoracoid, Rt	ISI A 91	Intercentrum (Caudal)	ISI A 136
Interclavicle	ISI A 9	Scapulacoracoid, Lt	ISI A 92	Intercentrum (Caudal)	ISI A 137
Left clavicle	ISI A 10	Scapulacoracoid, Lt	ISI A 93	Intercentrum (Caudal)	ISI A 138
Left clavicle	ISI A 11	Scapulacoracoid, Lt	ISI A 94	Intercentrum (Caudal)	ISI A 139
Right clavicle	ISI A 12	Ulna, Right	ISI A 95	Intercentrum (Caudal)	ISI A 140
Atlas	ISI A 13	Ulna, Right	ISI A 96	Intercentrum (Caudal)	ISI A 141
Four vertebrae	ISI A 14	Ulna, Left	ISI A 97	Intercentrum (Caudal)	ISI A 142
Three vertebrae	ISI A 15	Tibia, Right	ISI A 98	Intercentrum (Caudal)	ISI A 143
Right ischium	ISI A 16	Tibia, Left	ISI A 99	Intercentrum (Caudal)	ISI A 144
Left humerus	ISI A 17	Radius, Right	ISI A 100	Intercentrum (Caudal)	ISI A 145
Partial skull	ISI A 53	Fibula, Right	ISI A 101	Intercentrum (Caudal)	ISI A 146
Complete skull	ISI A 56	Neural spine	ISI A 102	Intercentrum (Caudal)	ISI A 147
Partial skull	ISI A 58	Neural spine	ISI A 103	Intercentrum (Caudal)	ISI A 148
Complete skull	ISI A 59	Neural spine	ISI A 104	Rib (Dorsal)	ISI A 149
Left mandible	ISI A 60	Neural spine	ISI A 105	Rib (Dorsal)	ISI A 150
Left mandible	ISI A 61	Intercentrum (Dorsal)	ISI A 106	Rib (Dorsal)	ISI A 151
Right mandible	ISI A 62	Intercentrum (Dorsal)	ISI A 107	Rib (Dorsal)	ISI A 152
Right mandible	ISI A 63	Intercentrum (Dorsal)	ISI A 108	Rib (Dorsal)	ISI A 153
Clavicle, left	ISI A 64	Intercentrum (Dorsal)	ISI A 109	Rib (Dorsal)	ISI A 154
Clavicle, left	ISI A 65	Intercentrum (Dorsal)	ISI A 110	Rib (Cervical)	ISI A 155
Interclavicle	ISI A 66	Intercentrum (Dorsal)	ISI A 111	Rib (Dorsal)	ISI A 156
Interclavicle	ISI A 67	Intercentrum (Dorsal)	ISI A 112	Rib (Dorsal)	ISI A 157
Humerus, Right	ISI A 68	Intercentrum (Dorsal)	ISI A 113	Rib (Dorsal)	ISI A 158
Humerus, Left	ISI A 69	Intercentrum (Dorsal)	ISI A 114	Rib (Dorsal)	ISI A 159
Humerus, Right	ISI A 70	Intercentrum (Dorsal)	ISI A 115	Rib (Caudal)	ISI A 160
Humerus, Right	ISI A 71	Intercentrum (Dorsal)	ISI A 116	Rib (Caudal)	ISI A 161
Humerus, Right	ISI A 72	Atlas with spine	ISI A 117	Rib (Dorsal)	ISI A 162
Humerus, Left	ISI A 73	Axis	ISI A 118	Rib (Dorsal)	ISI A 163
Humerus, Right	ISI A 74	Axis	ISI A 119	Rib (Cervical)	ISI A 164
Humerus, Right	ISI A 75	Axis	ISI A 120	Rib (Caudal)	ISI A 165
Humerus, Left	ISI A 76	Intercentrum (Dorsal)	ISI A 121	Rib (caudal)	ISI A 166
Ischium, Left	ISI A 77	Intercentrum (Dorsal)	ISI A 122	Phalange (post.right)	ISI A 167
Ischium, Right	ISI A 78	Intercentrum (Dorsal)	ISI A 123	Phalange (post.right)	ISI A 168
Ischium, Left	ISI A 79	Intercentrum (Dorsal)	ISI A 124	Phalange (post.right)	ISI A 169
Cleithrum, Left	ISI A 80	Intercentrum (Dorsal)	ISI A 125	Phalange (ant.right)	ISI A 170
Cleithrum, Right	ISI A 81	Intercentrum (Dorsal)	ISI A 126	Phalange (ant.right)	ISI A 171
Cleithrum, Left	ISI A 82	Intercentrum (Dorsal)	ISI A 127	Phalange (ant.right)	ISI A 172
Femur, Left	ISI A 83	Intercentrum (Dorsal)	ISI A 128	Phalange (ant.right)	ISI A 173
				Phalange (post.right)	ISI A 174

two main sets of the line canals, lateral and supraorbital, within the lachrymal. They are sinuous and touch each other inside the lachrymal.

The ratio of the width of the lachrymal at the orbit margin and the diameter of the orbit ranges between 0.2588 and 0.3409 in *B. maleriensis*. This ratio ranges from 0.6 to 0.4545 in case of *B. perfecta*. It appears that in *B. perfecta* the lachrymal is more equant and has a wider inser-

tion on the orbit margin (Case, 1922, fig. 1). This is evident also in "*B. howardensis*" (Sawin, 1945, fig. 3) and in "*Eupelor browni*" (Colbert and Imbrie, 1956, fig. 8) which were grouped into *B. perfecta* by Hunt (1993).

The curvature of otic notch, the shape of the tabular horn, the position and size of the orbits and the narial openings with respect to the skull length are also more uniform among the specimens of *B. maleriensis* than they are in *B.*



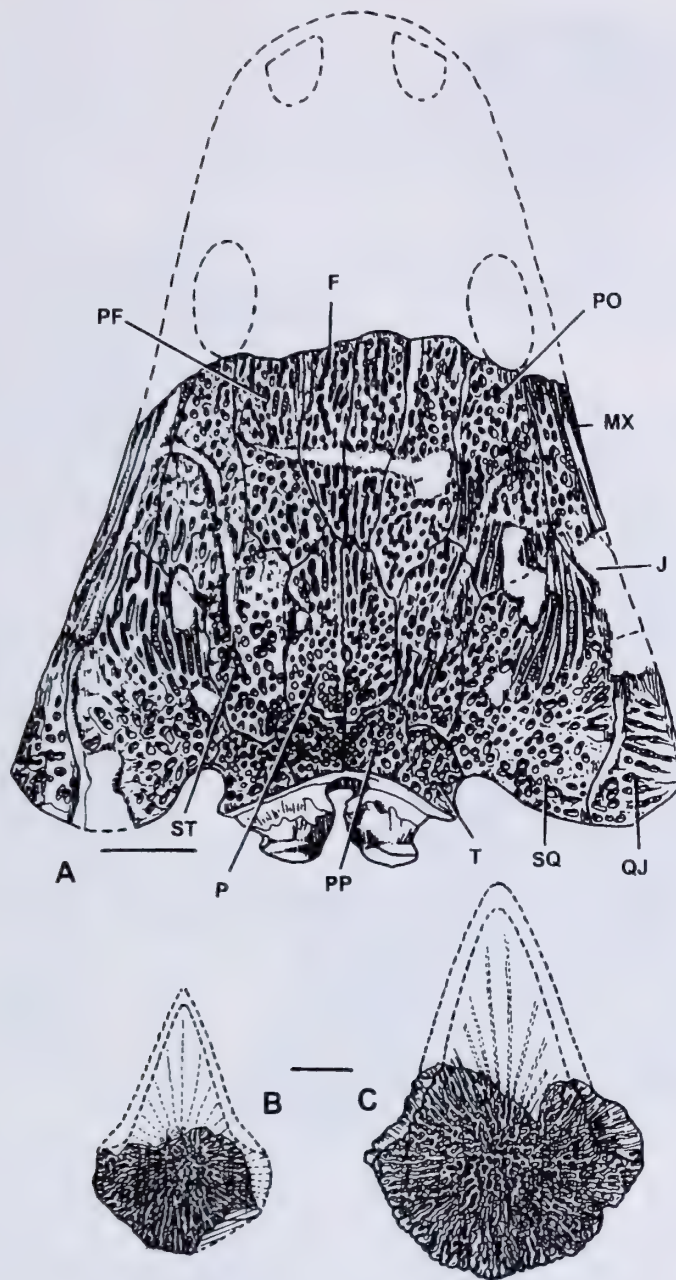
**Figure 5.** A = ISI A 56, skull roof of *Buettneria maleriensis*, new combination (abbreviations used are same as Figure 3). B = Occiput of *B. maleriensis*, based on the right side of ISIA 58. Abbreviations: EO = exoccipital; EOC = exoccipital condyle; FM = foramen magnum; OL = otic lamellae; PFM = paraquadrate foramen; PP = postparietal; PT = pterygoid; PTF = posttemporal fenestra; PTS = pterygoid sinus; Q = quadrate; QJ = quadratojugal; SQ = squamosal; XT = broken part of the stapes; T = tabular; TB = tubercle. Scale bars = 5 cm.

*perfecta*.

**Remarks.**—As discussed earlier, Hunt (1993) differentiated *Buettneria* from all other metoposaurids by the presence of the lachrymal in the orbit border. Other metoposaurids were further divided into several genera and species on the basis of certain synapomorphies and autapomorphies. For example, *Dutuitosaurus* and *Apachesaurus* share the apomorphy of having presacral centra with a diameter length < 0.8 cm and the former has the maxilla entering the orbit margin as an autapomorphy (Hunt 1993,

p. 80). For the genera which do not have the lachrymal in the orbit margin, the shape of the lachrymal was considered by Hunt (1993) to separate *Metoposaurus diagnosticus* from *Metoposaurus bakeri*. *Apachesaurus* has been partly characterised by the flexure of the supraorbital canal being separated from the lachrymal (Hunt, 1993, p. 81). However, all metoposaurids having their lachrymal in the orbit were grouped as *B. perfecta* by Hunt. The shape of the lachrymal or the position of the flexure of the supraorbital line canals or any other variations were not

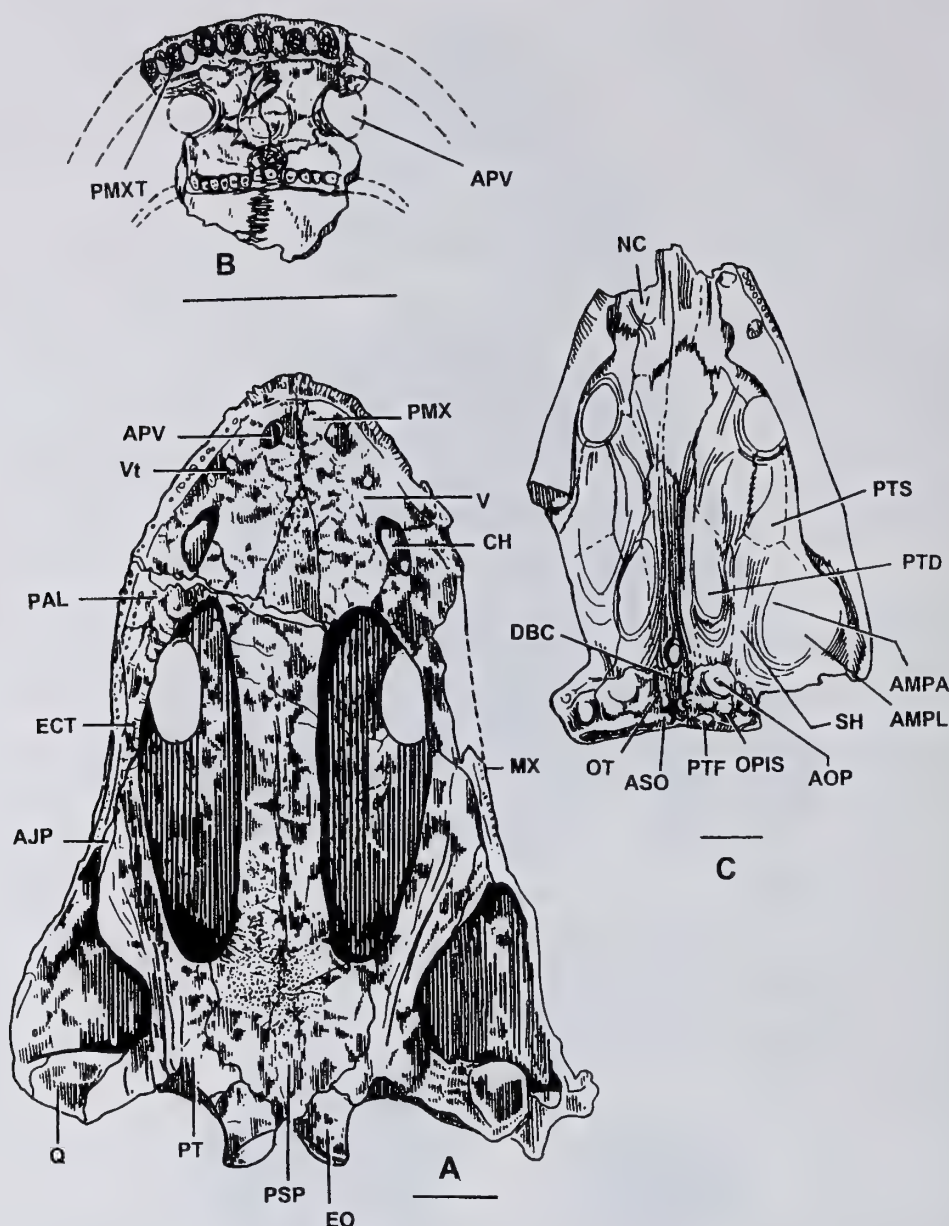




**Figure 6.** A = ISI A 53, skull roof of *Buettneria maleriensis*, new combination (abbreviations used are same as Figure 3). B, C = Interclavicles of *B. maleriensis*; B = collected from Tiki Formation (G.S.I. 2249, originally described by Lydekker 1885 as a skull roof bone), C = from Maleri (K33/638, Huene 1940). A, B and C are after Sengupta 1992. Scale bars = 5cm.

considered. Thus *Buettneria sensu* Hunt (1993) lacks any autapomorphy and results in a metataxon (Smith, 1994). Differentiating *B. maleriensis* from *B. perfecta* (*sensu* Hunt, 1993) on the basis of the width of the lachrymal at the orbit margin and the presence of the flexures of both the lateral and supraorbital line canals on the lachrymal is, therefore, relevant.

The localities yielding *B. perfecta* are restricted to the central and eastern United States, western Europe and northeastern Africa. During Late Triassic times these localities were believed to be very close and probably connected by land (Hunt, 1993, fig. 1). The population of *B. maleriensis* occurs outside that zone. Roychowdhury (1965) also emphasized the geographic isolation of the

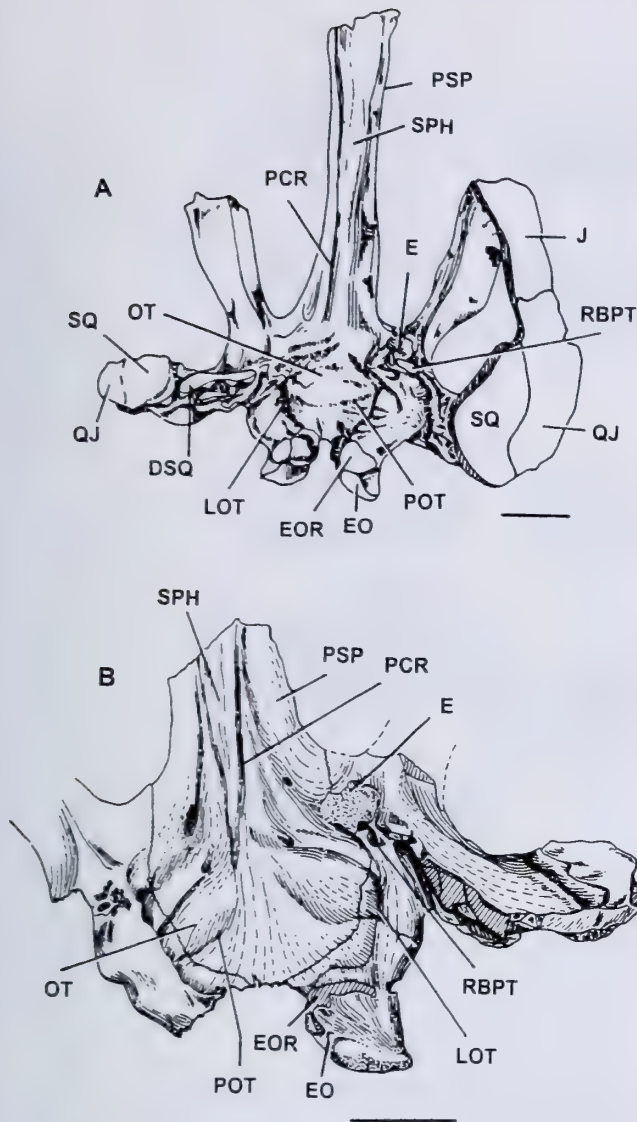


**Figure 7.** A = ventral view of the palate of *Buettneria maleriensis*, new combination based on ISIA 56. B = the anterior palatal vacuities and the straight row of teeth behind based on a supplementary fragment ISIA 56a collected from Nalapur. Note the detached tooth, complete and well preserved, cemented later on the vomer. C = ventral view of the skull roof of *B. maleriensis* based on ISIA 59. Abbreviations: AJP = alar process of the jugal; AMPA = adductor mandibulae, posterior articularis (after Wilson, 1941); AMPL = adductor mandibulae posterior longus (after Wilson, 1941); AOP = attachment for the cartilaginous otic process; APV = anterior palatal vacuity; ASO = attachment for the supraoccipital; CH = choana; DBC = dorsal side of cartilaginous brain case; ECT = ectopterygoid; EO = exoccipital; MX = maxilla; NC = dorsal impression of the nasal capsule (after Wilson, 1941); OT = otic capsule; PAL = palatine; PMX = premaxilla; PMXT = premaxillary teeth; PSP = parasphenoid; PT = pterygoid; PTD = deep portion of pterygoideus (after Wilson, 1941); PTF = posttemporal fenestra; PTS = superficial pterygoideus (after Wilson, 1941); Q = quadrate; SH = suspensorius hyoideus (after Wilson, 1941); V = vomer; Vt = vomerine tusk. Scale bars = 5 cm.

Indian population and suggested that biometric studies could reveal its specific characters. The biometric studies of Indian metoposaurids will be dealt in a separate publication. Meanwhile certain observations are noted below.

Colbert and Imbrie (1956, figs. 13, 14, p. 434-438, table 8) illustrated a technique to plot the bivariate population range diagram of certain skull roof parameters. The field range for *B. maleriensis* has been calculated using similar

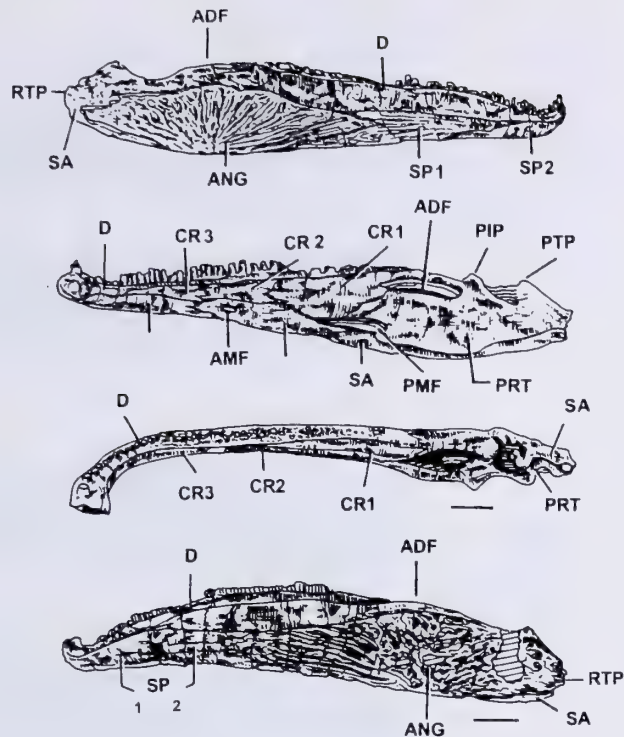




**Figure 8.** Dorsal view of the palate of *Buettneria maleriensis*, new combination; **A** = ISI A 59; **B** = ISI A 7, after Roychowdhury (1965). Abbreviations: DSQ = descending process of the squamosal; E = epipterygoid; EO = exoccipital; EOR = ascending process of the exoccipital (broken); LOT = lateral ridge bounding otic region; OT = otic capsule; PCR = ridge on the cultriform process of the parasphenoid; POT = posterior ridge bounding otic region; PSP = parashenoid; QJ = quadratojugal; RBPT = rim of the basiptyergoid process; SPH = depression for sphenethmoid; SQ = squamosal. Scale bars = 5 cm. B.

techniques. It is found that the range of *B. maleriensis* is specific and only partly overlapping with the multigeneric North American species now grouped together as *Buettneria perfecta* by Hunt (1993).

Sengupta and Ghosh (1993) attempted some cephalometric studies of some of the individuals of the North American metoposaurids and *B. maleriensis*. They used several skull roof parameters and extracted three major



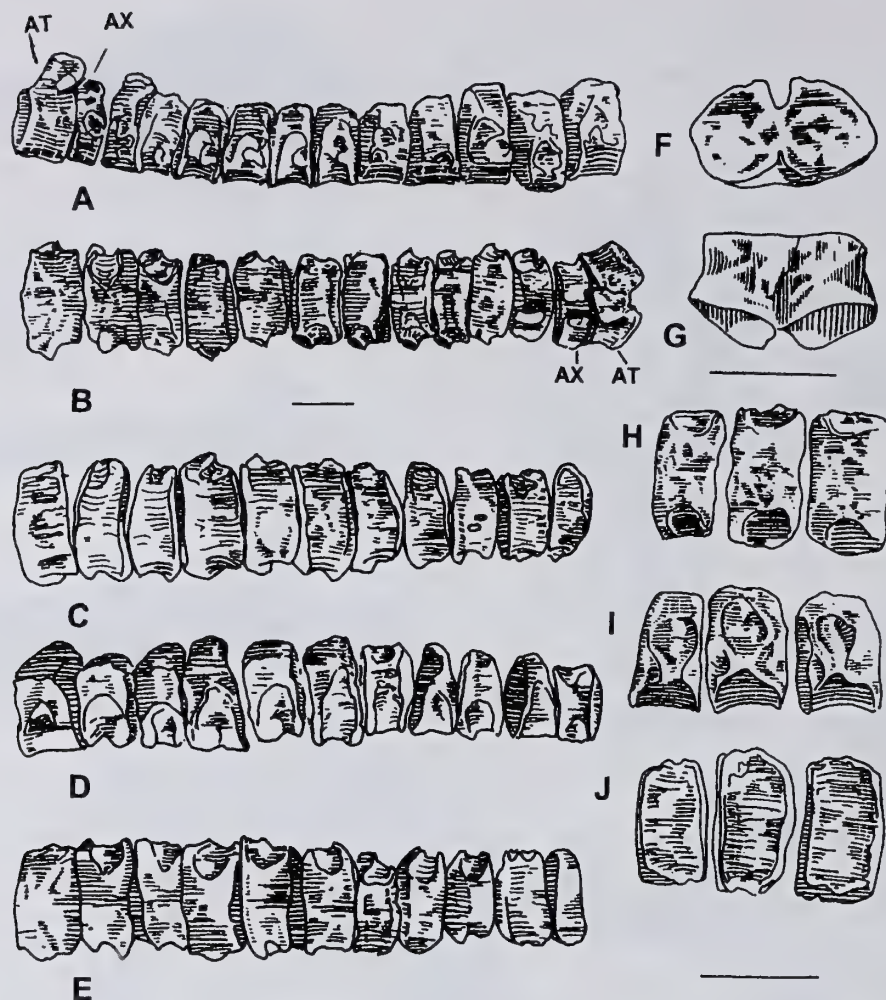
**Figure 9.** Right mandible of *Buettneria maleriensis*, new combination based on ISIA 60. From top: labial, lingual and dorsal views. Bottom: left mandible of *Buettneria maleriensis* based on ISIA 61. Abbreviations: ADF = adductor fossa; AMF = anterior Meckelian foramen; ANG = angular; CR (1,2,3) = coronoids; D = dentary; PIP = preglenoid internal process; PMF = posterior Meckelian foramen; PRT = prearticular; PTP = postglenoid process; RTP = retroarticular process; SA = surangular; SP (1,2) = splenials. Scale bar = 5 cm.

factors through a principal-component-based factor analysis. They found that the plots of the factor scores on two-dimensional Cartesian coordinates (Sengupta and Ghosh, 1993, fig. 2) indicate a peripheral position of the Indian metoposaurids with respect to the main concentration of the similar plots of the American metoposaurids.

#### General characters of *Buettneria maleriensis*

Osteology of both the dorsal and ventral sides of the skull roof and of the palate of the metoposaurids have been described in some detail by Cope (1868), Fraas (1889, 1913), Case (1922, 1932), Watson (1919), Sawin (1945), Romer (1947), Colbert and Imbrie (1956), Roychowdhury (1965), Dutuit (1976) and Hunt (1993) among others. Wilson (1941) discussed the soft parts. Hence only the general characters of the skull of *B. maleriensis* are given below.

**Skull roof.**—*Buettneria maleriensis* has a very flat skull with short snout and anterolaterally placed orbits (Figures



**Figure 10.** Elements of vertebral columns of *Buettneria maleriensis*, new combination. **A** = lateral and **B** = dorsal views of one possible presacral column; **C** = dorsal, **D** = lateral and **E** = ventral views of second such pre sacral column. AT and AX are the atlas and the axis. Another single atlas with anterior (**F**) and dorsal (**G**) views are also shown. **H**, **I** and **J** are the dorsal, lateral and ventral views of a set of three adjacent caudal intercentra. All the specimens were collected from the Aigerapalli accumulation. Scale bars = 5 cm.

1A-C; 2A, B; 3; 4; 5A; 6A). Skulls have well defined, curved tabular horns and deep otic notches. The pineal foramen is placed well posterior to the orbit. The postparietal is shorter than the parietal.

The posterior part of the skull has rather thick rectangular bones, namely the tabular, postparietal, parietal and supratemporal, which are strongly ornamented with circular pits walled by high ridges.

The snout, with close, large nares, is also well built with a similar type of ornament. Premaxilla and nasal are the two major bones in this area. Roychowdhury (1965) noted the presence of an extra bone in one of the specimens (ISI A 4) of *B. maleriensis* exposed on the dorsal surface of the skull. No such bone has been identified in any of the newly collected specimens. This is probably the extra

sutural growth noted in many temnospondyls (Romer, 1947; Welles and Cosgriff, 1965). The floor of the naris is made up of the septomaxilla which is thin and flat.

The middle part of the skull table is flat, thin and has elongate bones, namely, the frontal, postorbital, prefrontal and jugal with elongate ridges and valleys as ornament. The lateral line canals do not form a loop posterior to the orbit. The lachrymal becomes narrow and touches the orbit margin.

**Palate.**—The ventral side of the palate (Figure 7A, B) has a flat rectangular base composed of parasphenoid from which a triradiating structure emerges with two palatine rami of the pterygoid between sub temporal and interpterygoid vacuities and a wide, flat cultriform process of the parasphenoid in the middle. The latter connects the base





**Figure 11.** Ribs (left side) of *Buettneria maleriensis*, new combination based on specimens ISIA 149 to ISIA 166. The total number of cervical, thoracic, sacral and caudal ribs are not known. In the diagram, only the preserved specimens are arranged one after another (external view at the top and internal view at the bottom). **A** = one of the two cervical ribs preserved. **B** = a typical anterior thoracic rib; **C** = posterior thoracic rib; **D** = possibly the lone sacral rib and **E** = caudal rib. Scale bar = 5 cm.

of the parasphenoid to the wide vomers. On the ventral side of the skull roof a narrow ridge is present in the midline particularly in the postorbital part (Figure 7C). This tapers towards the anterior and is perforated by the pineal foramen. This ridge corresponds in position to the depression present on the dorsal side of the cultriform process of the parasphenoid. This depression probably housed the cartilaginous sphenethmoid (Figure 8).

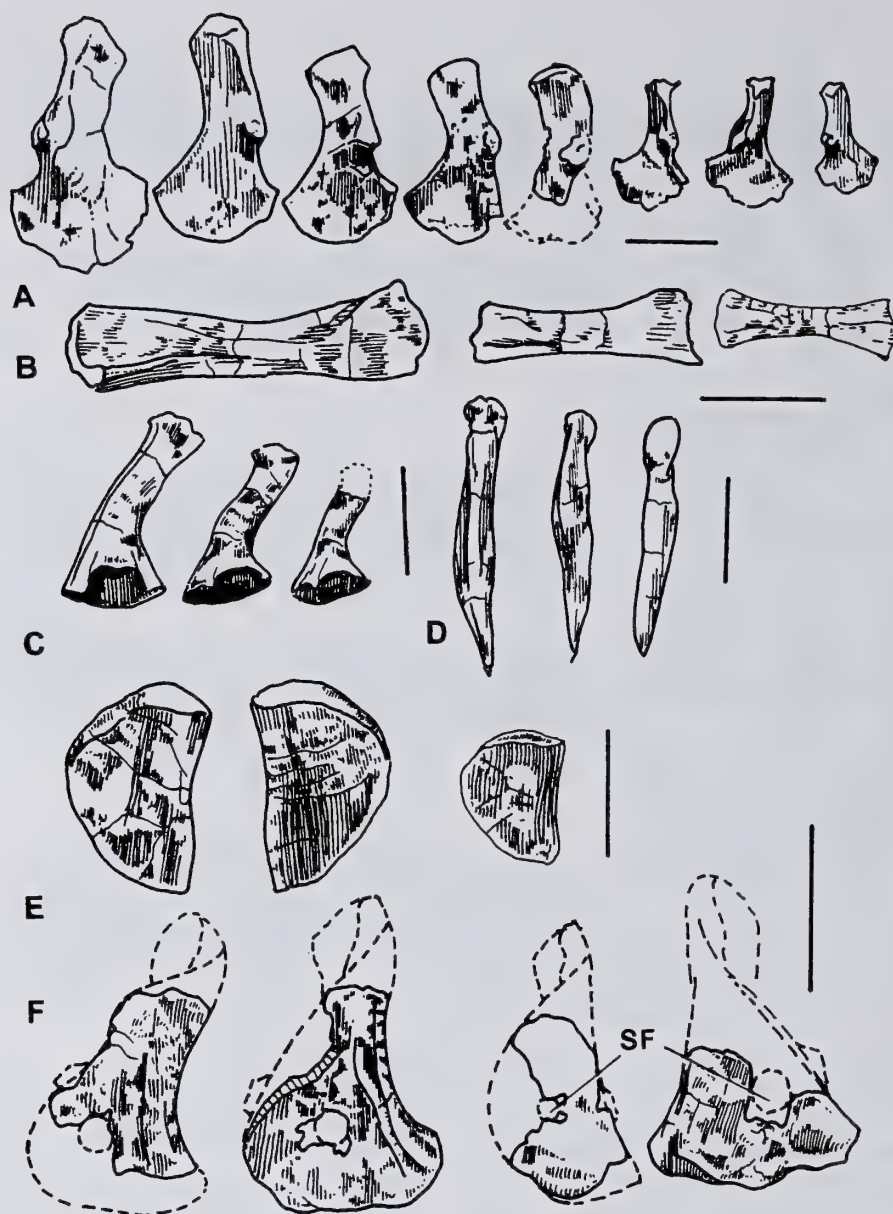
The position of the epipterygoid and the foramen of the internal carotids, the recess for the basiptyergoid process, the anterior end of the depression for the sphenethmoids and the position of the arcuate ridges bordering the otic region on the dorsal side of the palate of *B. maleriensis* are figured (Figure 8). These features, however, are similar in all the metoposaurids (see Case, 1922, figs. 2, 3; Wilson, 1941, figs. 1, 2; Roychowdhury, 1965, fig. 12; DuTuit, 1976, pls. 11–15).

On the dorsal side of the pterygoid, in ISI A 59, a part of the epipterygoid is preserved (Figure 8A, B). The ascend-

ing process of the epipterygoid was previously illustrated by Roychowdhury (1965, p 28). The braincase and associated features, the position of the epipterygoids and adjacent canals shown by Roychowdhury (1965), Case (1922) and DuTuit (1976) are noted in almost all the new specimens of *B. maleriensis*. Similar braincases are partly preserved in ISI A 7 and ISI A 59. The stapes is partly preserved in two individuals, ISI A 56 and ISI A 58 (Figure 5B).

**Maxillary and palatal dentitions.**—Maxillary and palatal dentitions extend far posterior to the centre of the interpterygoid vacuities. Vomerine and palatine tusks are present. One of the paratypes (ISI A 56a) has two well developed, circular, well separated, anterior palatal vacuities and a series of small vomerine teeth posterior to them (Figure 7A, B).

**Occiput.**—The occiput has the shape of a triangle with the base made up of postparietal and tabular on the dorsal side (Figure 5B). The exoccipital sutures with the postparietal and tabular housing a small, circular posttem-



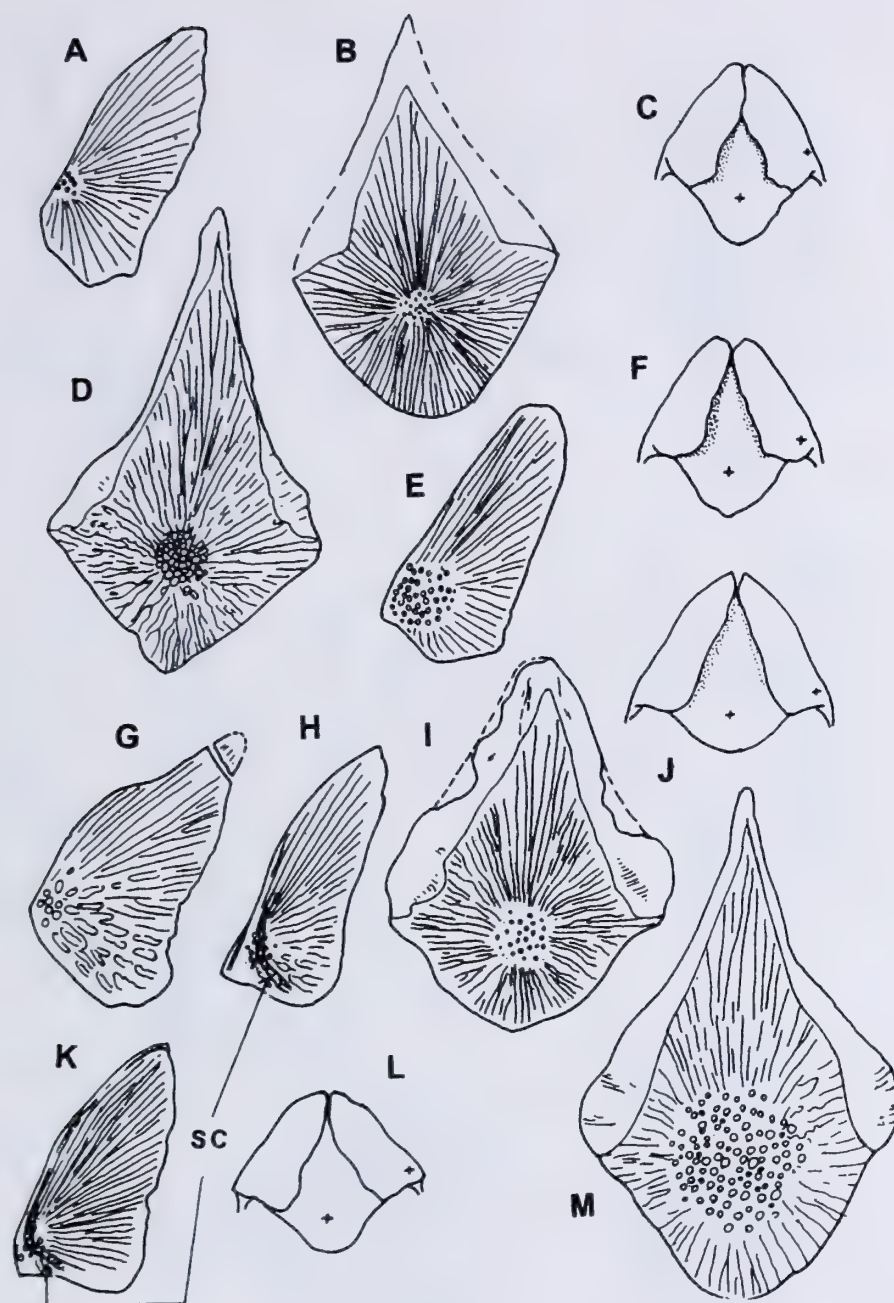
**Figure 12.** Some of the postcranial bones of *Buettneria maleriensis*, new combination, collected from the Aigerapalli metoposaur graveyard. **A** = Humeri, ventral view (ISIA 69 to 76), **B** = Femora, ventral view (ISIA 83 to 85), **C** = Ilii, lateral view (ISIA 86 to 88), **D** = Cleithra, mesial view (ISIA 80 to 82), **E** = Ischia, dorsal view (ISIA 77 to 79) and **F** = Scapulocoracoids, mesial view (ISIA 89, 90, 92, 94) with supraglenoid foramen (SF). Scale bars = 5 cm.

poral fossa at the junction of the three bones. The foramen magnum is at the centre of the triangle which is terminated by the flat parasphenoid and occipital condyles almost at the same ventral level. There is a little vaulting of the pterygoid and the ascending processes of the bone sutures with the quadratojugal and squamosal. These bones form the dorsal margin of a large, elliptical paraquadrate foramen. Unlike the earlier composite reconstruction of the occiput (Roychowdhury, 1965, fig. 11, p. 21), the speci-

mens described here show a thin insertion of the pterygoid in the lateral part of the paraquadrate foramen.

**Mandible.**—The mandible of *B. maleriensis* is described here for the first time. Two complete mandibles and a few broken fragments are available for study (Figure 9). The specimens are deepest in the region of the angular and their cross-sections are squared at the midlength. One of the specimens (ISIA 60) is more cylindrical in cross-section and narrow at the region of the penials. The mandible has

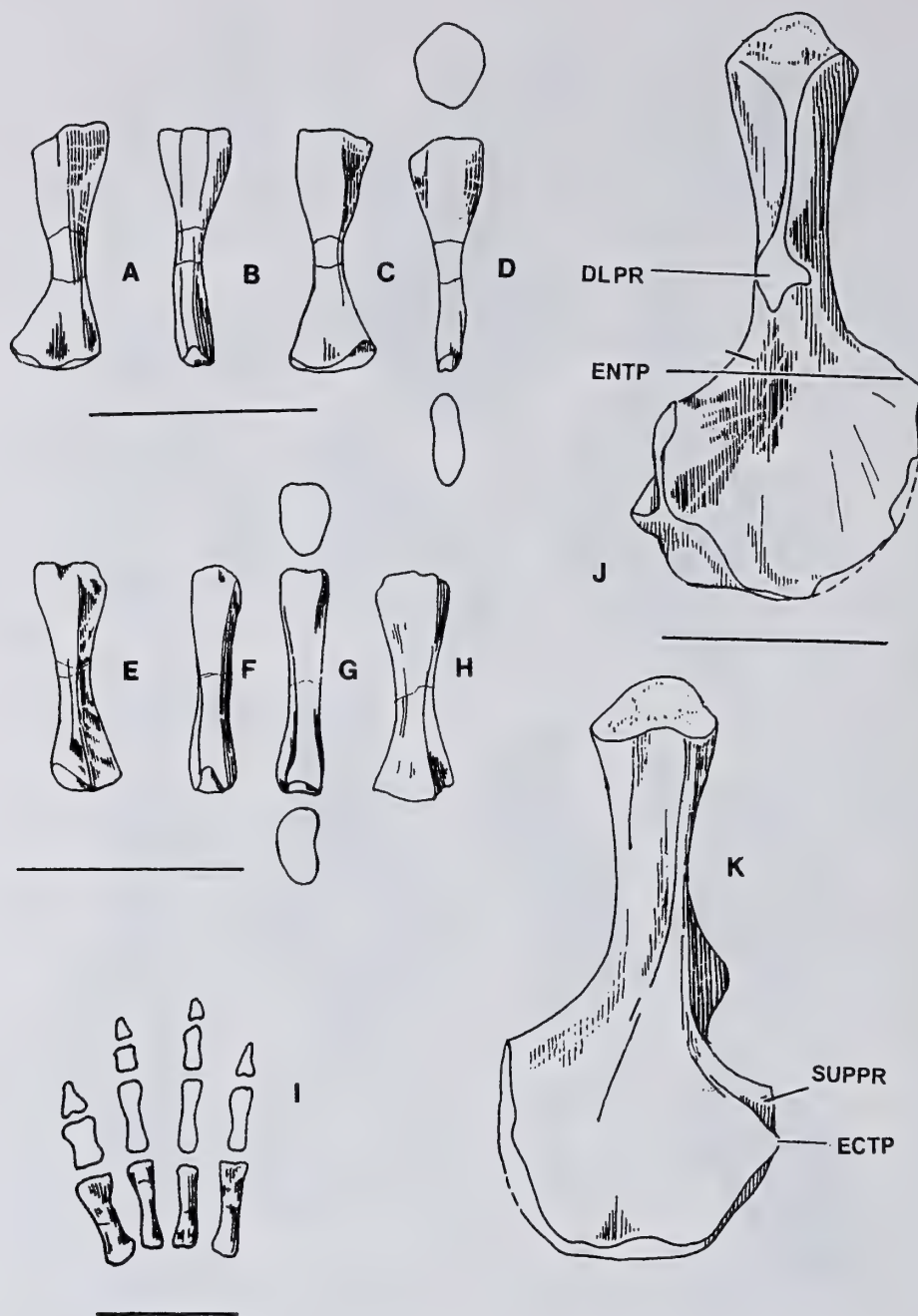




**Figure 13.** Clavicles and interclavicles of *Metoposaurus diagnosticus* Fraas, 1913 (A = clavicle; B = interclavicle; C = clavicle interclavicle together); "*Buettneria howardensis*" Sawin, 1945 (D = clavicle; E = interclavicle; F = clavicle interclavicle together); *B. maleriensis*, new combination, (G = clavicle; H = clavicle; I = interclavicle; J = clavicle interclavicle together); "*M. ouazzouri*" Dutuit, 1976 (K = clavicle; L = clavicle interclavicle together; M = interclavicle); Sc = sensory canal. For *B. maleriensis* two different types of clavicles are shown (G and H). C; F and L are after Wernerburg (1990). Diagrams are schematic (not in scale) as interclavicles are enlarged (compared to respective clavicles) to illustrate the ornament.

a short retroarticular process with articular, surangular and prearticular exposed on the dorsal surface. Jupp and Warren (1986) described this as the type of postglenoid area noted in some temnospondyls including metopo-

saurids. The angular is the dominant bone of the labial side. On the lingual side a large, elongate posterior Meckelian foramen is present whose anterior border is formed by the posterior coronoid. The adductor fossa is

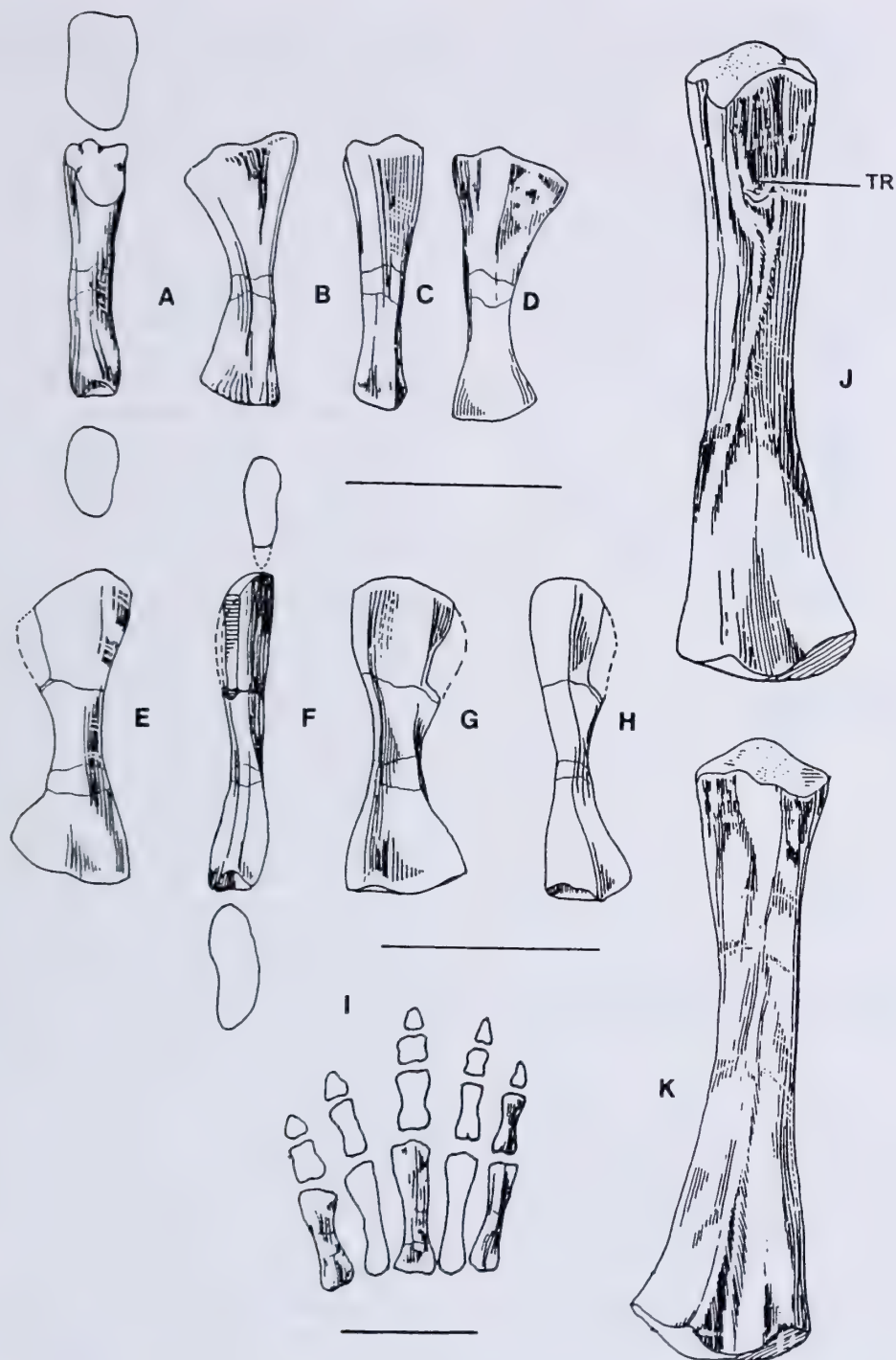


**Figure 14.** Right radius of *Buettneria maleriensis*, new combination, **A** = external, **B** = anterior, **C** = internal, **D** = posterior views and right ulna **E** = external, **F** = anterior, **G** = internal, **H** = posterior views (based on ISIA 100 and ISIA 95 respectively). **I** = digits of manus of the right side (ISI A 170, to 173, phalangeal formula based on Dutuit, 1976). Right humerus based on ISIA 68; **J** = Ventral, **K** = Dorsal views. DLPR = Deltoidial process; ECTP = ectepicondyle; ENTP = entepicondyle; SUPPR = supinator process. Scale bars = 5cm.

large and elliptical. No coronoid process is present. There is a large circular depression around the symphyseal tusk which forms part of the dentary tooth row. A small row of teeth is present on the inner side of the circular depression.

*Vertebral elements.*—All metoposaurids have typical discoid intercentra of different sizes and shapes (Figure 10). The overall shapes vary from circular to triangular and sometimes these variations are associated with their position in the vertebral column. Variations are also noted

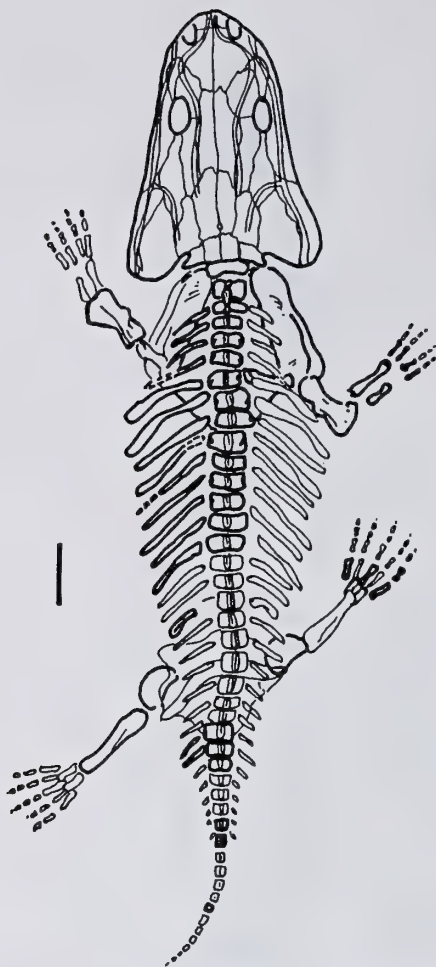




**Figure 15.** Left tibia of *Buettneria maleriensis*, new combination, **A** = posterior, **B** = internal, **C** = anterior, **D** = external and right fibula, **E** = posterior, **F** = internal, **G** = anterior, **H** = external. (based on ISIA 99 and 101 respectively). Pes of the right side (based on ISI A 167, 168, 169 and 174). Phalangeal formula based on Dutuit (1976). Left femur based on ISIA 83; **J** = ventral, **K** = dorsal views; TR = trochanter. Scale bars = 5 cm.

among individuals. The vertebral count of an individual of the metoposaurids is uncertain. Sawin (1945) figured 18 presacral intercentra for *Buettneria*. Dutuit (1976) illus-

trated 22 intercentra for one individual of "*M. ouazzoui*" (XIII /14/66) and 20 for another (XIII /4/66). In the reconstruction of *B. maleriensis* an average of 20 presacral



**Figure 16.** Composite restoration of *Buettneria maleriensis*, new combination. Dark lines represent elements from one individual. Scale bar = 10cm.

intercentra have been figured. The new collection from Aigerapalli includes 23 dorsal and 13 caudal intercentra. From the accumulation of vertebral elements of at least six individuals, parts of two possible columns (Figure 10) are reconstructed from the presacral vertebrae following Sawin (1945) and Dutuit (1976).

The atlas is double faceted at the anterior end to host the double condyles (Figure 10A, B, F, G). In one of the two inferred vertebral columns just mentioned (Figure 10A) the axis and one intercentra (possibly occurring just behind the axis) have two rib facets on the lateral side. In some of the intercentra the facets protrude whereas in larger intercentra (which are possibly further down the trunk), the posterior presacrals have only the facet without the neck. Anterior to the facet there is another curvature. In lateral view these two curvatures form an hourglass-like depression. This is more pronounced in the caudal intercentra (Figure

10I). The caudals are triangular in outline, quite flat on the dorsal side, platycoelous to opisthocelous and smaller in size (Figure 10H–J). Sawin (1945) figured a sacral intercentrum which really differs little from some of the presacrals of the Indian taxon.

In one axis, a space created by the underside of the base of the posteriorly depressed neural arch and the scooped posterior dorsolateral part of the intercentrum clearly indicates the shape of the pleurocentrum. In another specimen, parts of the plerocentrum are preserved. Dutuit (1976) described one vertebra of "*M. ouazzoui*" where both the intercentrum and pleurocentrum are preserved and the combined centrum looks like a discoid with a slightly off-centered notochordal perforation. This type of vertebra has also been observed in *Compsoceros cosgriffi*, an Indian chigutisaurid (Sengupta, 1995). However, no such pleurocentral ossification is noted in *B. maleriensis*.

Unfortunately all the specimens in the collection have their neural arches broken. The axis has the base of the neural arch preserved in some specimens. An intervertebral position of the arches has been predicted by some authors (e.g. Roychowdhury, 1965; Dutuit, 1976; Warren and Snell, 1991). However, there is no direct evidence for this in the specimens of *B. maleriensis*.

**Ribs.**—The total number of ribs present is uncertain. Two cervical, several anterior presacral and some abdominal ribs have been found (Figure 11). One possible sacral and few caudal ribs are also present.

The cervicals have two separate facets or rib heads. The presacral rib heads are elliptical with capitulum and tuberculum connected by a narrow extension. The postsacral ribs have triangular or even squarish heads. The anterior presacral units have flattened distal extensions with uncinate processes. The abdominal ribs are cylindrical and lack the uncinate process. Warren and Snell (1991) noted that temnospondyls possess a single sacral rib which is expanded both proximally and distally and is stout and short. One short, curved and distally expanded rib is figured here as a possible sacral ribs (Figure 11D). It has a rather expanded proximal end but is quite thin. The caudals are shorter, curved and pointed distally.

**Elements of the pectoral girdle.**—The scapulocoracoid and the cleithrum are new additions to the Indian metoposaurid collections. They have the usual characters of metoposaurids (Dutuit, 1976). The clavicle and interclavicle have already been described (Roychowdhury, 1965). The scapulocoracoid has an enclosed supraglenoid opening (Figure 12F). This was considered as a primitive character (Warren and Snell, 1991). The cleithrum is spoon-shaped with dorsal expansions (Figure 12D).

**Clavicle and interclavicle.**—Roychowdhury (1965) noted two different types of clavicles in the Indian metoposaurids. He also mentioned that the clavicles of *M. diag-*



*nosticus* have a long contact anterior to the interclavicle which is not seen in *B. maleriensis*. Sengupta (1992) illustrated two similar-looking interclavicles, one from the Tiki and the other from the Maleri Formation which are redrawn here (Figures 6B, C). Colbert and Imbrie (1956) used the difference in the position of the centre of ossification and the variable nature of the clavicle-interclavicle overlap as taxonomically important characters. This variability was also highlighted by Warren and Snell (1991) and Werneburg (1990). Figure 13 indicates the clavicles and interclavicles of different metoposaurid taxa with variations in the ornament, position of the centre of ossification and nature of overlap of the clavicle on the interclavicle. However, ISI A 12 as illustrated by Roychowdhury (1965, figure 18), has a unique shape. A sensory canal is present in the clavicles of the Indian metoposaurids. This was also noted in *M. ouazzoui* (Dutuit, 1976).

*Ilium and ischium*.—The ischium is a semicircular bone and the ilium is elongate with a dorsal blade which is rather thick (Figure 12C). Warren and Snell (1991) considered this as a character of taxonomic value.

*Fore limbs*.—The humerus, like all other metoposaurid humeri, is well built, twisted and has pronounced processes for muscle attachments (Figure 14J, K). The ulna (Figure 14A–D) and radius (Figure 14E–H) are similar to the ones described by Dutuit (1976) for the metoposaurids from Morocco. Some digits of the right manus were also found (Figure 14I).

*Hind limbs*.—The femur, figured for the first time here (Figure 15J, K), is rather long and fully ossified with complete distal and proximal articular surfaces. The areas for *trochanters* are well developed. The tibia (Figure 15A–D), fibula (Figure 15E–H) and some digits of the right pes (Figure 15I) are also figured. The proximal and distal end of the tibia and fibula are less expanded than in "*B. howardensis*" as figured by Sawin (1945).

A composite restoration of *B. maleriensis* is shown in Figure 16.

### Aspects of taphonomy

*Buettneria maleriensis*, as stated earlier, is known from a large number of specimens from the Maleri Formation of the Pranhita-Godavari valley. Its occurrence in the Tiki Formation of the Son Mahanadi valley is rare. Hence emphasis is given here to the geology and the nature of occurrence of *B. maleriensis* in the Maleri Formation.

*Geological attributes*.—Mudstone, sandstone and peloidal calcarenite/calcirudite of various colours of the Maleri Formation crop out in NW-SE trending linear belts (Figure 17). The overall dip is 12 to 18 degrees towards the NE. The paleocurrent direction is towards the north.

The mudstone is dominantly red in colour and is structureless. Smectite is the major constituent of the clayey part (Sarkar, 1988). Haematite crystals are also common and iron oxide is responsible for the red colour (Robinson, 1970). The mudstones are exceptionally rich in vertebrate fossils. The sandstone is usually calcareous, cross-bedded, fine- to coarse-grained, containing weathered feldspars and infrequent garnets. Rock fragments and clay galls of different size, shape and colours are common. Fining-upward sequences are discernible in the sandstones (Sarkar, 1988). The sand bodies form narrow elongate ridges with mudstone valleys in between.

The peloidal calcarenite/calcirudite occurs either as solitary mounds and/or a string of such mounds within the red mudstone and also at the bottom of the sandstone (Sarkar, 1988, p. 267). The peloidal calcarenite/calcirudites are cross-bedded with overlapping troughs of various magnitudes and comprise calcite-cemented spherical or discoid peloids of micrite or microsparry calcite. According to Sarkar (1988) the paucity of broken abraded peloids and other evidences indicate a local pedogenic origin of the peloids.

Sengupta (1970) noted that while the mudstones represent the interchannel facies, the sand bodies are deposited in the channels of a meandering river system flowing north in a large valley trending NW-SE. Maulik and Chaudhuri (1983) described such sandbodies as ephemeral channel fills.

*Palaeoclimate*.—Pascoe (1959) suggested that the Maleri sediments were deposited in an extremely arid environment. Robinson (1970) first noted that the red mudstones of the Pranhita-Godavari valley were not necessarily deposited in desert like conditions. The Maleri vertebrate fauna indicates a well watered country. The colour of the mudstone is imparted by iron oxides and the high content of ferric oxides and presence of haematite crystals indicate an oxidising environment of deposition. Recent works suggest that the red colour may be remotely linked with climate (Pye, 1983). The absence of many dessication cracks and footprints as well as the occurrence of fewer evaporites indicate that the climate was not arid. This is also supported by the presence of unionids and an array of aquatic or amphibious vertebrates. The paucity of plants was previously considered as an indicator of aridity. However, this is negative evidence and a good number of herbivore remains are found. On the other hand, the high smectite content (Sarkar, 1988) may indicate low rainfall (Singer, 1980). Peloidal calcirudite and arenite are also indicative of reworking of older soil profiles (Sarkar, 1988). To explain the contrasting evidence it is suggested that there was possibly seasonality in the climate. The aquatic members of the Maleri fauna, living in ephemeral rivers, had survived the drier situations by concentrating in the more permanent bodies of water (Robinson, 1971; Chatterjee *et al.*,



1987).

*Mode of occurrence.*—Animals living in the lowland habitat are mostly found in the floodplain deposits of the Maleri Formation (Kutty, 1971). Though exact proportions are difficult to determine, the number of lowland metoposaurids are always more than those of the robust rhynchosaurs and phytosaurs. The floodplains were well watered with a good drainage as remains of lowland or semiaquatic vertebrates are found there, associated with occasional bivalves, fossil wood and other sporadic plant debris, within thick red-coloured mudstones (Behrensmeyer and Hook, 1992).

Fossils are found as cracked, flaked or distorted bones which are often covered by peloidal calcirudite and calcarenite and calcareous concretions. Various stages of bone weathering (Behrensmeyer, 1982) are also present in the fossilized bones of the Pranhita-Godavari valley (Sengupta, 1990). The transported, disarticulated, abraded bones indicate large time gaps between their death and burial (Behrensmeyer and Hook, 1992).

In most of the red beds of the Maleri Formation vertebrate remains occur chiefly as surface accumulations of stray fragments and also as *in situ* bones in the floodplains. The *in situ* bones, in turn, can be fragmentary or complete. Four taphonomic facies can be identified in the Maleri sediments. The vertebrate bones occur as 1) complete *in situ* material in the mudstone, 2) fragmentary but *in situ* material in mudstone, 3) well preserved but broken bone accumulation in the sandbodies or in the peloids and 4) stray surface accumulation in the mudstones. Types 2 and 3 can be subdivided into i) isolated but broken skeletal parts and ii) fragments of one or more skeletal elements.

Bones belonging to metoposaurids are found in all these types of accumulations. Most of the metoposaurid material described by the early workers like Miall (1875), Lydekker (1885) and Huene (1940) belonged to taphonomic facies 4. Voorhies (1969) noted three major groups of bones according to their potential for dispersal particularly by water. The bulk of the specimens of *B. maleriensis* belong to Voorhies' (1969) group which constitutes an assemblage of skulls and mandibles. This indicates the transported nature of the metoposaurid material from the Maleri Formation. The most common skull fragments are of the tabular area as it is the strongest. The jaws are frequently represented by the symphyses. The skull margins are often preserved, without the thin midskull region. The deposition of peloidal calcirudites of diagenetic origin on the bones indicates various orders of reworking.

The above taphonomic picture indicates that, after death, the semiaquatic and lowland fauna of the Maleri Formation, living in a seasonal climate, were mostly exposed on the flood plains and were fragmented and transported (and even reworked). The lowermost mudstone

unit of the Maleri Formation is the thickest (Figure 17) and there the remains of lowland vertebrates are high in number. In that unit, due to some events leading to mass accumulations, finds like Aigerapalli came into being. A closer look at the Aigerapalli site may reveal some more information.

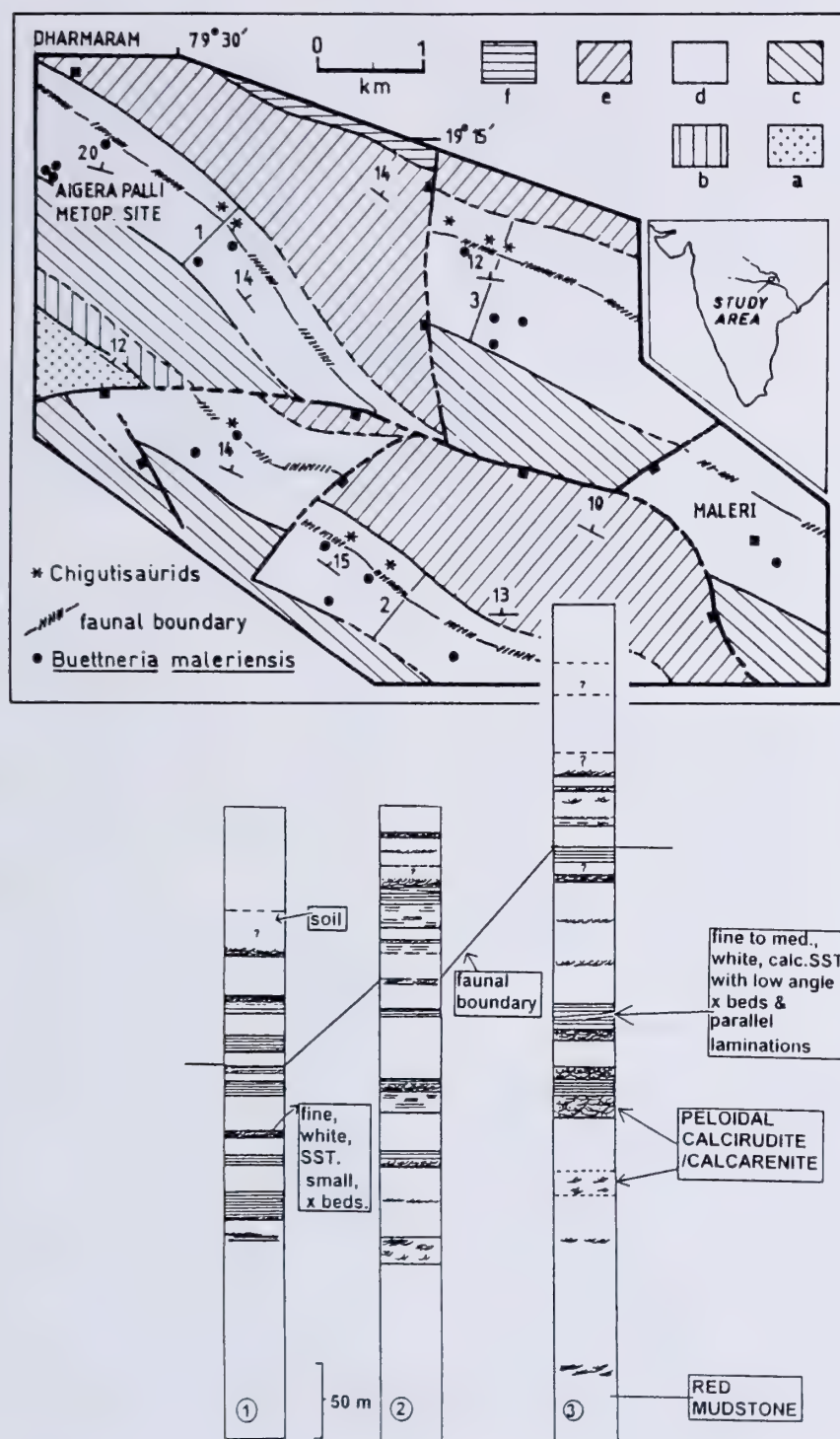
*Taphonomy of the Aigerapalli accumulation.*—The Aigerapalli site, near the base of the basal mudstone, chiefly comprises mudstones of red colour, with a few streaks of white, calcareous, fine- to medium-grained well-sorted sandstone. The bones were excavated from an area of only 10 m by 5 m which yielded over 100 disarticulated bones of several individuals.

There are 9 humeri (6 from the right side and 3 from the left) from six individuals with three different size ranges (Figure 12A). As indicated by the size ranges, two individuals were larger in size, one intermediate and three were small. The larger humeri come in the size range of 12.6 to 11.5 cm in length. There are three such specimens (a left and two from right) from two individuals. The next size range is a left and a right humerus of around 10 cm length possibly representing another individual. The last size range is around 6 cm length and from 4 specimens (three from left and one right) at least three individuals can be identified. The three size domains are also supported by the length of the three femora (Figure 12B). However, two skulls were recovered of which one is complete.

Though the thickest mudstone unit of the Maleri contains the metoposaur accumulation, sporadic occurrence of peloidal calcarenites/rudites within the unit suggests intermittent exposure to aridity. In fact, it is argued in the section dealing with paleoclimate that contradictory evidence for aridity and humidity are present in the lithology and fauna of the Maleri Formation and a seasonal climate could be a possible explanation. The aquatic fauna survived in small deeper pools at the time of aridity and might have moved away in search of safer places (Robinson, 1971, Chatterjee *et al.*, 1987). While doing so they could be trapped in the thick mud. Their remains were buried after being scattered by various agents. The bones have evidences of some amount of transportation. On the other hand, some of the small postcranial as well as a number of small and delicate teeth are well preserved. Hence, the transportation was possibly not prolonged.

The Aigerapalli type of bone accumulation is not uncommon at other metoposaurid-yielding localities around the world (Romer, 1939; Dutuit, 1976). The absence of articulated individuals is marked in the Aigerapalli and also in the mass accumulation of metoposaurids in the Lamy amphibian quarry in New Mexico (Romer, 1939). The latter has a similar taphonomic background to Aigerapalli where hydrodynamic sorting of bones of dead individuals from a residual pool affected by drought has been thought





**Figure 17.** Geological map around the villages of Maleri and Dharmaram. Legends: a = Kamthi Formation, b = Yerrapalli Formation, c = Bhimaram Formation, d = Maleri Formation. Within the Maleri Formation the boundary between the lower and upper Maleri fauna is shown. The lines 1, 2 and 3 represent the positions of the columnar sections shown below the map.

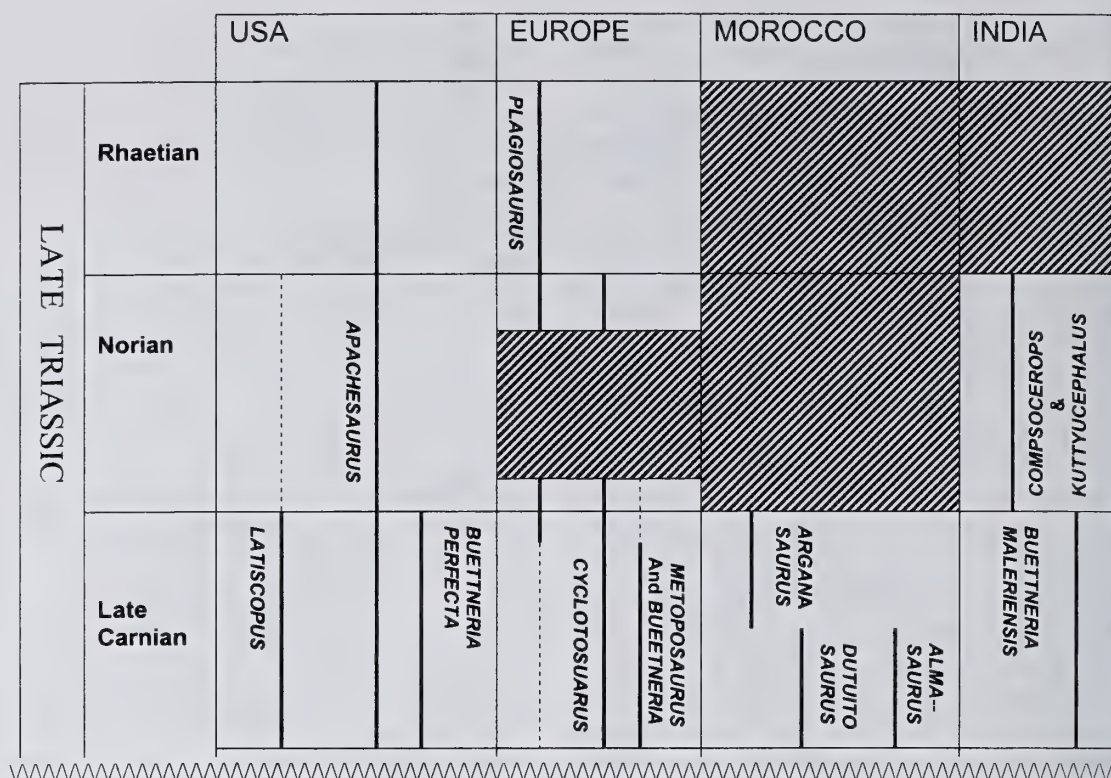


Figure 18. Stratigraphic ranges of metoposaurids and other associated temnospondyls of the Late Triassic Period.

to be the reason behind the accumulation (Romer, 1939; Hunt and Lucas, 1989)

#### Stratigraphic range of *B. maleriensis*

Roychowdhury (1965) suggested that the Maleri fauna is Carnian or early to middle Norian in age. Subsequently Kutty and Sengupta (1989) divided the Maleri fauna into two groups, a lower and an upper. The age of the lower group, which includes *B. maleriensis*, was stated as Late Carnian. The fauna associated with *B. maleriensis* chiefly consists of the phytosaur *Parasuchus* (*Paleorhinus*), the rhynchosaur *Paradapedon*, the theropod *Alwalkeria*, the protorosaur *Malerisaurus*, the cynodont *Exeraetodon*, an aetosaur and a large dicynodont. Hunt (1993), following the scheme of Lucas and Hunt (1989), put the lower Maleri fauna into the early part of the Late Carnian. The presence of *Paleorhinus* which is found from Tuvulian marine strata of Austria and stands as a good marker fossil in continental deposits, helped to infer this age (Hunt and Lucas, 1991).

Lucas (1998), stated that palynostratigraphy, sequence stratigraphy and magnetostratigraphy of the Chinle Group indicate a Late Carnian age and the principal correlatives are the lower Maleri, Schilfsandstein, Kieselsandstein, and

Blasensandstein of the German Keuper and the Argana fauna of Morocco. There is dispute also whether the lower Maleri fauna is early Late Carnian as stated by Hunt (1993) and Hunt and Lucas (1991) or late Late Carnian as stated by Kutty and Sengupta (1989). Hunt and Lucas (1991) predicted the age of the lower and upper Maleri faunas on the basis of phytosaurs. The Upper Maleri phytosaurs are yet to be described in detail. Moreover, immediately above the upper Maleri the Lower Dharmaram fauna (Kutty and Sengupta, 1989) also has an undescribed phytosaur and one or more aetosaurs. Bandyopadhyay and Roychowdhury (1996) noted that *Rutiodon*-like phytosaurs are found only from the upper Maleri and the age of the immediately overlying lower Dharmaram could be Late Norian. This suggests an Early Norian age for the upper Maleri fauna confirming the late Late Carnian age of the lower Maleri fauna occurring immediately below. Hence, it is likely that the last appearance datum of *B. maleriensis* is late Late Carnian.

Except in North America all metoposaurids were restricted to the Carnian. In North America, the Dockum Formation of Western Texas, Bull Canyon and Redonda Formations of Eastern New Mexico, the Painted Desert Member of the Petrified Forest Formation and the Owl



Rock Formation of northeastern Arizona have metoposaurids younger than Carnian in age. The post Carnian metoposaurid, *Apachesaurus*, is not abundant compared to the Carnian occurrences (Hunt, 1993). From the South-western United States, Long and Murry (1995) noted "a definite replacement of large metoposaurids by smaller ones" during the Early Norian. No small temnospondyls like *Apachesaurus* (Hunt, 1993) and *Latiscopos* (Wilson, 1948) from North America or *Almasaurus* (Dutuit, 1976) from Morocco are found in the Late Triassic deposits of Europe or India. On the other hand, no brachyopid temnospondyl, with parabolic skull and deep palate with downturned pterygoids, has been described from the North American Late Triassic (Figure 18). Such temnospondyls are represented in Europe by the plagiosaurids (Kuhn, 1932; Milner, 1994) and in India by the chigutisaurids (Sengupta, 1995).

#### **Paleoposition of India and aspects of paleogeography, paleoclimate and faunal migration**

Metoposaurids are restricted chiefly to latitude 40 to 60 North, with the exceptions being the Indian occurrences. The distance of the latter from the other localities was, however, minimised to some extent by the union of the continents during the Late Triassic. On the other hand, chigutisaurids are thought to have originated in Australia (Warren and Hutchinson, 1983) and are so far found to be restricted to Gondwana. India is the only place where metoposaurids were replaced by the chigutisaurids. This has led to some interesting observations on the paleoposition of India and some aspects of paleoclimate, paleogeography and faunal migration.

The absence of endemism among the Late Triassic Indian tetrapods has long been known (Colbert, 1958; Chatterjee and Hotton, 1986). Cox (1974) noticed that the similarity coefficient of Indian fauna with that of North America and Europe is quite high (59% and 81% respectively). On the other hand that with Africa and South America is also not negligible (75% and 56%).

Smith and Briden (1977; map 13, p. 24) have shown that, during the Triassic, Australia was close to India and so were Europe and North America. The circum-Tethyan shoreline is short and curved and the position of Africa was such that the land distance between India and North America was minimal. The figures shown by Hay *et al.* (1982) indicate the position of India was almost halfway between North America and Australia at the end of the Triassic.

Cox (1974) noted that in the Triassic there were no major climatic barriers. Robinson (1973) postulated a sharply seasonal rainfall in parts of North America, Europe, Africa and India during the Triassic (Robinson, 1973, fig. 10).

Parrish *et al.* (1982, fig. 5, p. 39) have also shown that during Induan time a low pressure belt was located in Africa with an adjacent high in the north of India and another one in Europe causing a similar type of wind flow in the areas close to the Tethys. The entire area had 100 to 200 units of rainfall (Parrish *et al.*, 1982) without any major climatic barrier. The Late Triassic metoposaurids could have come from Laurasia along the circum-Tethyan shoreline to India as a geographically peripheral group (this could also support the contention that the Indian metoposaurid, *B. maleriensis*, is a distinct taxon). Chigutisaurids, on the other hand, arrived later, either from Australia or South America.

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# Permian bivalves from the H. S. Lee Formation, Malaysia

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**Abstract.** Three bivalve species collected from the Permian H. S. Lee Formation at the H. S. Lee No. 8 Mine in Perak, Malaysia are described. They are identified as *Sanguinolites ishii* sp. nov., *Megalodon (Megalodon) yanceyi* sp. nov., and *Myalina (Myalina)* cf. *wyomingensis* (Lea). The fossil locality is famous for the abundant occurrence of gastropods together with bivalves, cephalopods, calcareous algae and others, but is flooded and inaccessible now. The new species of *Megalodon* is considered to be the first record of the genus in the Permian.

**Key words:** H. S. Lee Formation, Malaysia, *Megalodon*, Permian bivalves

## Introduction and previous research

The bedrock of open-pit tin mines in the Kampar area, Perak, Malaysia is mostly composed of carbonate rocks, such as limestone, dolomitic limestone, and dolomite. The fossiliferous limestone beds occupying the uppermost interval of this sequence occur in the H. S. Lee and Nam Long Mines, and were named the H. S. Lee Beds by Suntharalingam (1968). The rich Permian fossils collected from the H. S. Lee Mine (mostly No. 8 Mine, the type locality of the formation) are described by various authors. They were first reported by Jones, Gobbett, and Kobayashi in 1966, then by Suntharalingam (1968). In addition to abundant and diverse gastropods, common bivalves, cephalopods, scaphopods, brachiopods, chitons, corals, sponges and calcareous algae were listed. Fusulinids were reported by Ishii (1966), calcareous algae by Elliot (1968), *Prodentalium* by Yancey (1973), one chiton and 91 gastropod species in 52 genera by Batten (1972, 1979, and 1985), and two ammonoid species by Lee (1980).

Concerning the bivalves, the morphology and taxonomic position of large bizarre shells of alatoconchid bivalves were discussed by Runnegar and Gobbett (1975), Boyd and Newell (1979), Yancey (1982), Yancey and Boyd (1983), and Yancey and Ozaki (1986). Ten other bivalve species were described by Yancey (1985). According to Runnegar and Gobbett (1975) and Yancey (1985) molluscan fossils are abundant in the upper 15 m of the formation. A 3–5 m-thick alatoconchid zone is sandwiched between gastropod-rich limestones. Bivalves are mainly contained in the alatoconchid zone and are not common in the gastropod-rich limestones. Ten species of bivalves belonging to eight genera are enumerated in Yancey (1985):

*Grammatodon (Cosmetodon) obsoletiformis* (Hayasaka)  
*Grammatodon (Cosmetodon)* sp.  
*Shikamaia perakensis* (Runnegar and Gobbett)  
*Saikraconcha (Dereconcha) kamparensis* Yancey and Boyd  
*Saikraconcha (Dereconcha)* sp.  
*Prospodylus chintongia* Yancey  
*Pernopecten malaysia* Yancey  
*Palaeolima* sp.  
*Lyroschizodus* sp.  
*Permartella quadrata* Yancey

The age of the H. S. Lee Formation is confirmed by fusulinids and ammonoids. The upper part of the formation contains the fusulinid *Misellina claudiae* and the lower part contains *Pseudofusulina krafftii* (Ishii, 1966). According to Runnegar and Gobbett (1975), *Pseudofusulina krafftii* is found 10 m below the alatoconchid beds. Ishii correlated both fusulinid intervals to the *Misellina* subzone (the lower subzone of the *Parafusulina* zone) in South China (Sheng, 1963), and the *Misellina claudiae* zone in Japan, which was considered to be equivalent to the *Pseudofusulina ambigua* zone and *P. krafftii* zone by Kanmera (1963). Based on these fusulinids the age of the H. S. Lee Formation is assigned to the late Bolorian in the Tethys or the late Kungurian Stage in the Urals and probably correlates with the late Leonardian in the United States. Lee (1980) identified three ammonoid species in the H. S. Lee Formation, *Adrianites* cf. *insignis* Gemmellaro, *Neocrinites* cf. *guanxiensis* Chao and Liang, and *Prostacheoceras skinneri* Miller, and considered the age of the formation to be Artinskian or early Guadalupian (probably late Artinskian). The fossil evidences of both groups indicates an age of latest Cisuralian (Early Permian) or early Guadal-



Figure 1. Index map showing the fossil locality (asterisk).

pian (Middle Permian) of the three-fold division of the Permian (Wardlaw, 2000).

Yancey (1985) pointed out the close similarity of the bi-valve assemblage to that of the Akasaka Limestone in central Japan, which contain *Shikamaia akasakensis* Ozaki, *Grammatodon obsoletiformis* (Hayasaka), *Lyroschizodus japonicus* (Hayasaka) and others. The Akasaka Limestone is one of the members of the accretionary complex believed to be shifted from the tropical region (Nakazawa, 1991). It ranges from the *Parafusulina* Zone up to the *Codonofusiella-Reichelina* Zone. The above-mentioned bivalves are found in the *Neoschwagerina* Zone (Murgabian). Accordingly, the Malaysian fauna is a little earlier in age than that of the Akasaka Limestone fauna.

The materials examined in the present paper were collected by Ishii from the horizon just above the alatoconchid zone at the H. S. Lee No. 8 Mine (Figure 1). They are part of a collection given to Kyoto University in 1970, which contains the type specimen of *Prospendylus chintongia* described by Yancey (1985). In addition, *Sanguinolites ishii* sp. nov., *Megalodon* (*Megalodon*) *yanceyi* sp. nov., *Myalina* (*Myalina*) cf. *wyomingensis* (Lea), *Permartella quadrata* Yancey, and *Grammatodon* (*Cosmetodon*) *obsoletiformis* (Hayasaka) are identified in the collection. The first three taxa are described below. The occurrence of *Megalodon* is most remarkable, because the genus has not

previously been reported in the Permian. Furthermore, the H. S. Lee No. 8 Mine was flooded and the exposures are no longer accessible (Runnegar and Gobbett, 1975). Therefore, the above-mentioned species are worthy of description. All the specimens are kept at the Kyoto University Museum.

### Systematic description

Order Pholadomyoida Newell, 1965

Family Grammysiidae S. A. Miller, 1977

Genus *Sanguinolites* M'Coy, 1844

### *Sanguinolites ishii* sp. nov.

Figure 2A, B

**Materials.**—A pair of incomplete right and left valves, holotype HP100027.

**Etymology.**—Dedicated to Ken-ichi Ishii who collected the fossils and offered them to Kyoto University.

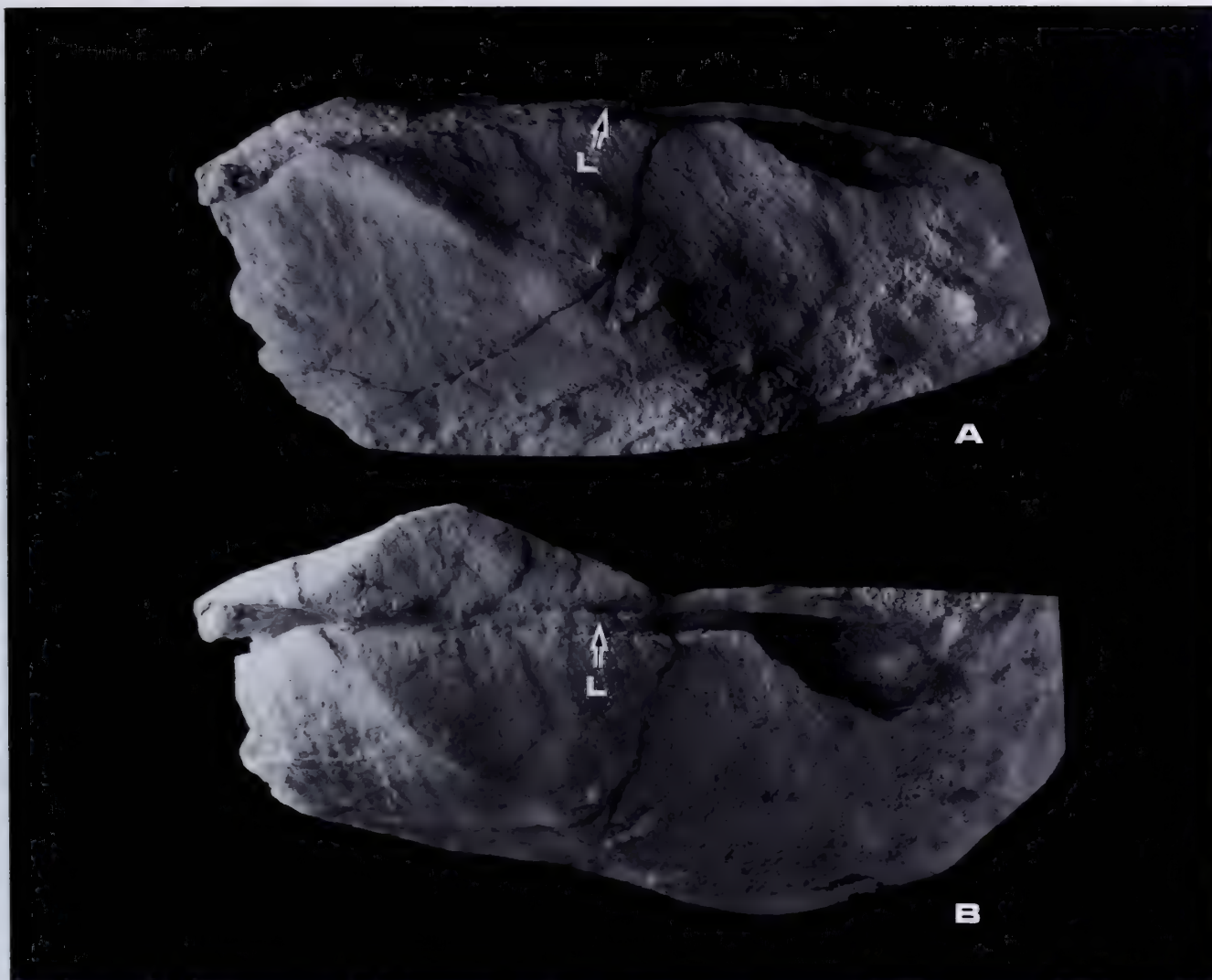
**Diagnosis.**—Large *Sanguinolites* with posteriorly expanded shape, weak ventral sinus, and relatively weak umbonal ridge.

**Description.**—Shell large, equivalve, inequilateral, elongate, trapezoidal, more than 115 mm long, 45 mm high, and about 15 mm deep, more than twice as long as high, a little expanded posteriorly; umbo subdued, prosogyrate, slightly projecting above hinge margin, lying at anterior one-fifth of shell length; umbonal ridge weak, rounded, becoming obsolete with growth; hinge line straight, ventral margin weakly sinuous, anterior margin well rounded, and posterior margin truncated with rounded posteroventral corner; lunule deep and narrow; escutcheon probably absent; long, opisthodontic ligament well preserved; hinge edentulous; surface covered with weak, sometimes rugose, growth lines. Anterior and posterior gape of shell uncertain.

**Discussion.**—A part of the anterior area and the posteroventral area in the left valve are not preserved, and only part of the dorsal margin of the right valve is visible. However, the general shape can be judged by growth lines. The dorsal margin of the shell is thickened and contains a shallow furrow which receives the external ligament. Although the escutcheon is not observed and the concentric sculpture is weak, the present specimen is considered to belong to the genus *Sanguinolites* based on the other characteristics, such as elongate outline, very anteriorly located umbo, presence of umbonal ridge, long opisthodontic ligament, edentulous hinge, and concentric ornament.

This species is similar in shape to *Sanguinolites kamiyasensis* Nakazawa and Newell (1968, p.42, pl. 11, figs. 3, 4) reported from the lower Middle Permian in Japan, but differs in its much larger size, weaker umbonal ridge and the absence of radial ornaments on the posterodorsal area.





**Figure 2.** A, B. *Sanguinolites ishii* sp. nov., holotype (HP 100027). A. Left valve, lateral view; B. Oblique dorsal view of joined left and right valves, both in natural in size. L = calcified ligament.

The Upper Devonian *Sphenotus* (= *Sanguinolites*) *tiogensis* McAlester (1962, p. 62, pl. 26, figs. 1–14) is more similar to the present species in shape and size, but is distinguished from the latter in its stronger rugose concentric sculpture.

Order Hippuritoida Newell, 1965

Superfamily Megalodontoidea Morris and Lycett 1853

Family Megalodontidae Morris and Lycett, 1853

Genus *Megalodon* Sowerby, 1827

Subgenus *Megalodon* Sowerby, 1827

*Megalodon (Megalodon) yanceyi* sp. nov.

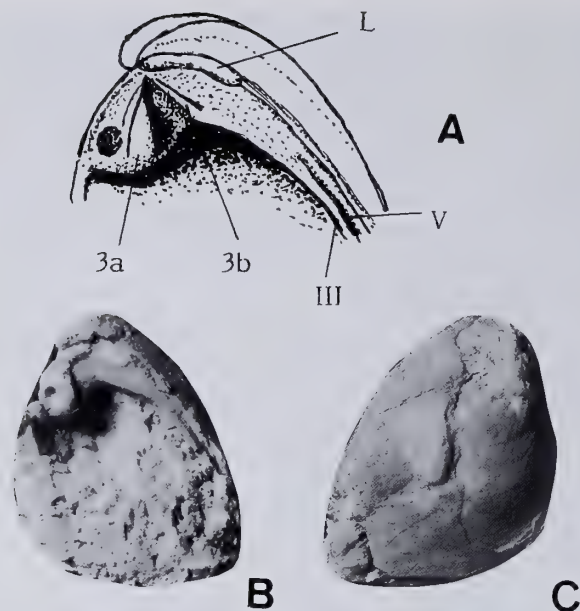
Figures 3A–C, 4A–F

**Materials.**—Nearly complete, left and right valves. Right valve, holotype HP100025; left valve, paratype HP100026. (After the manuscript was accepted, the posteroventral part of the holotype specimen was accidentally damaged as shown in Figure 4A–C).

**Etymology.**—Dedicated to Thomas Yancey for his contribution to the study of the molluscs of the H. S. Lee Formation.

**Diagnosis.**—A Permian species of *Megalodon* characterized by relatively unmodified cardinal hinge, and one posterior lateral tooth in the left and two in the right valve.

**Description.**—Shell medium in size, equivalve, inequilateral, subtrigonal in shape, inflated, spirogyrate, strongly carinate posteriorly with a sharp umbonal ridge; angle be-



**Figure 3.** *Megalodon (Megalodon) yanceyi* sp. nov. A. Sketch showing the hinge of right valve,  $\times 1.5$ . Abbreviations: 3a and 3b, anterior and posterior cardinal teeth; III and V, posterior lateral teeth; L, ligament. B, C. Holotype specimen (HP100025) before damage, B,  $\times 1.0$ , C,  $\times 1.0$ .

tween posterior area and flank of shell about  $90^\circ$ ; posterior area having a weak radial furrow; hinge plate thick, hinge of right valve consisting of a strong, trigonal, anterior cardinal tooth (3a) with a weak radial groove, a very weak, rudimentary, posterior cardinal tooth (3b), and two, long, posterior lateral teeth (III and V) running parallel to posterodorsal margin; cardinal area of left valve poorly preserved, but judging from cardinal sockets of left valve, hinge of right valve consisting of a round, anterior cardinal tooth (4a) and a strong, trigonal, posterior cardinal tooth (2) with uneven surface and a posterior lateral tooth (IV) which is inserted between two posterior lateral teeth of right valve and continues into wide nymph; ligament external, opisthodontic, well preserved; surface of both valves covered with dense growth lines; muscle scars not observed.

**Discussion.**—The dental formula (Bernard, 1895) of the present species is shown as

3a	3b	III	V
4a	2	IV	

The external shape and the dentition indicate that this species belongs to *Megalodon (Megalodon)* Sowerby (the type species of the genus is a Devonian species, *M. cucullatus* Sowerby; see Newell, 1969, N743 m, fig. E215–4). The details of dental features of the genus are rather variable. The Malaysian species is especially similar to *Megalodon (Megalodon) abbreviatus* (von Schlotheim) (= *cucullatus*)

described by Haffer (1959, p. 149, fig. 6; p. 150, pl. 12, figs. 13, 14), who discussed the hinge character of the genus in detail. However, the cardinal plate of the described species is less robust and the cardinal hinge is less modified than the latter.

**Measurements.**—Right valve, HP100025, length 39.0 mm, height 31.0 mm, umbonal length from anterior end of shell 8.0 mm, depth 13.0 mm, height/length ratio 1.26, depth/length ratio 0.26, maximum shell length 41.0 mm; left valve, HP100026, length 40.0 mm, height 32.0 mm, umbonal distance from anterior end of shell 9.0 mm, depth 15.0 mm, height/length ratio 1.25, depth/length ratio 0.23, maximum shell length 42.0 mm.

Order Pterioidea Newell, 1965  
Suborder Pteriina Newell, 1965  
Family Myalinidae Frech, 1891  
Genus *Myalina* de Koninck, 1842  
Subgenus *Myalina* de Koninck, 1842

*Myalina (Myalina) cf. wyomingensis* (Lea, 1853)

Figure 4G, H

*Compared with.*—

*Modiolus wyomingensis* Lea, 1853, p. 205, pl. 20, fig. 1a.

*Myalina wyomingensis* (Lea). Girty, 1903, p. 422, pl. 8, figs. 8–13.

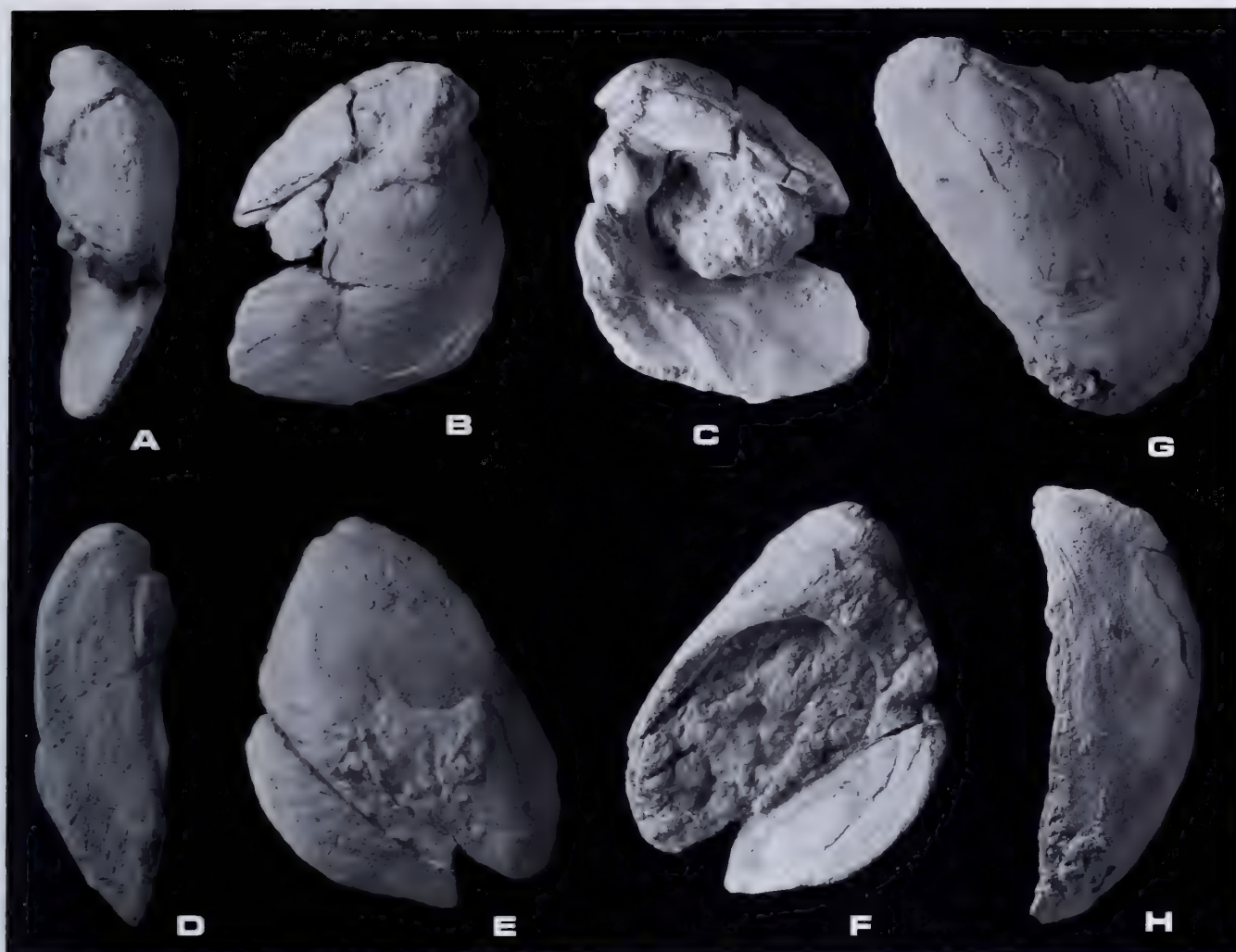
*Myalina (Myalina) wyomingensis* (Lea). Newell, 1942, p. 49, pl. 3, figs. 1–4, 7, 10; pl. 7, fig. 6.

**Material.**—One nearly complete left valve, HP100028.

**Description.**—Shell medium in size, prosocline, changing in shape from *Promytilus* type to *Myalina* type through ontogeny; highly vaulted, umbonal ridge prominent and rounded with umbonal angle increasing from  $45^\circ$  in early growth stage to  $75^\circ$  in adult; 35 mm long, 37 mm high, and 17 mm deep, greatest dimension 43 mm; anterior lobe well developed, anterior margin slightly sinuated, hinge margin straight and nearly equal to shell length; surface covered with close-set growth lines, occasionally developed into lamellae; hinge unknown.

**Discussion.**—Although the hinge of the shell cannot be observed, the present species is quite similar to *Myalina (Myalina) wyomingensis* (Lea) found from the Desmoinesian to Wolfcampian in the United States, and it is difficult to separate the two species from each other based on the external shape, but the Malaysian species seems to be less oblique and a little higher than the American *M. wyomingensis*.





**Figure 4.** A-F. *Megalodon (Megalodon) yanceyi* sp. nov. Posterior (A), lateral (B), and interior (C) views of right valve of the holotype (HP100025) after damage. Posterior (D), lateral (E), and interior (F) views of left valve of the paratype (HP 100026), cardinal area poorly preserved. Calcified ligament is observed in both valves. G, H. *Myalina (Myalina) cf. wyomingensis* (Lea). Lateral (G) and anterior (H) views of left valve (HP100028). All figures  $\times 1.5$ .

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my gratitude to him. Lastly, I appreciate reviewers' valuable suggestions and refinement of my English.

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# Systematic position and palaeoecology of a cavity-dwelling trilobite, *Ityophorus undulatus* Warburg, 1925, from the Upper Ordovician Boda Limestone, Sweden

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**Abstract.** The high level systematic position and autecology of the Upper Ordovician cavity-dwelling trilobite *Ityophorus undulatus* is discussed. The lectotype is here selected from syntypes. The Late Cambrian family Loganellidae Rasetti, 1959 appears to contain the ancestors of this species. *Ityophorus* is compared with the closely related Middle Ordovician trilobite *Frognaspis* to pick out the stable characters. These are the yoked free cheeks, the wide cephalic doublure in combination with a distinct narrow cephalic rim, pygidial pleural and interpleural furrows, and a smooth mesial part of the inner cephalic doublural margin (lack of an embayment of the hypostomal suture). Because of the presence of several characteristics unique to the two, they are best attributed to a subfamily Ityophorinae, which is interpreted as a relict group of the Loganellidae. The discussion of the autecology is based on the structural relationship of the mouth opening and position of basal podomeres in relation to the cephalic margin, and on the functional morphology of terrace lines on the brim margin. The appendages appear to have been long to reach the substrate. The cephalon appears to have held the body rigidly by means of the terrace lines. This made it possible for the animal to use its appendages freely, for instance, in scratching the substrate. Some cavities in the present study area show evidence of a gel-like consistency of the cavity walls, which best fits the behavior mentioned above. *Ityophorus* is interpreted to have been an animal adapted to cavities rich in bacterial mats, on which it may have fed.

**Key words:** cavity dwelling, *Ityophorus undulatus*, life habit, Loganellidae, structural relationship, Trilobita, yoked free cheeks.

## Introduction

The term “cryptic habit” denotes an adaptations into a buildup environment, which usually provides cohesive substrates with the potential to provide cavities. Caves in recent reefs, which offer spaces for cryptic modes of life, occasionally are dominated by sponges and cryptic bacteria (Reitner, 1993). With these, bivalves, gastropods and arthropods form cryptic biotopes. From a classificatory point of view, some cavity-dwelling metazoans appear to be phylogenetically relict groups (relict biota), or groups which retain primitive morphological characters (Hayami and Kase, 1996; Hobbs, 2001). This trend should have been characteristic also of ancient cavity dwellers in buildups, although no vagile metazoan fossil group has ever been recognised as a “relict group” so far.

The Upper Ordovician minute trilobite species *Ityophorus undulatus* Warburg, 1925, which is of uncertain position in high-rank systematics (Kaesler, 1997, p. 302), is commonly found in patches of internal sediment in

autochthonous taphonomical conditions (Suzuki and Bergström, 1999, fig. 10), commonly associated with micro-gastropods. The sediment is characteristic of the “stromatolite cavity” system which is a common sedimentary structure in Palaeozoic carbonate mud mounds. Thus Suzuki and Bergström (1999) concluded that the present species was a cavity dweller. This rare mode of occurrence, which is defined correctly as a cavity setting, offers us an unusual chance to examine if a fossil species of cryptic habit has a similar mode of adaptation to recent examples or not.

The aims of the present study are to examine the high-rank systematic position of *Ityophorus undulatus*, to present an example of morphological transformations in a trilobite caused by environmental pressure, and to discuss the autecology from functional and sedimentological points of view.

## Geological setting

*Ityophorus undulatus* occurs in the Upper Ordovician Boda Limestone, Siljan district, Sweden. This unit

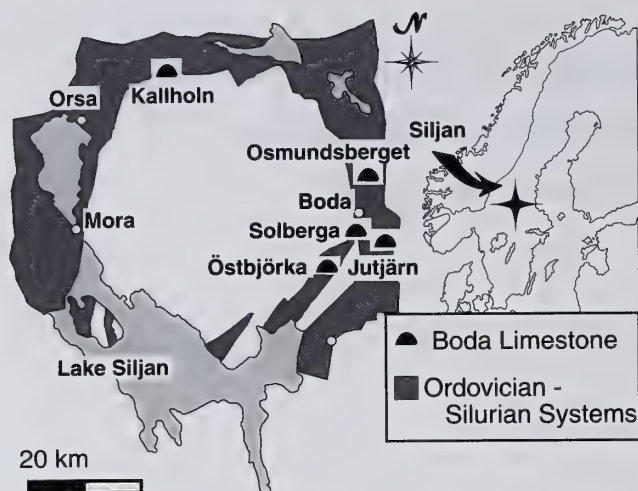


Figure 1. Locality map of some Boda Limestone bodies.

consists of a set of carbonate buildup masses of which now up to 20 are known in the Siljan district of Sweden (Figure 1; Jaanusson, 1979). The thickness and the diameter of an isolated Boda Limestone body are said to be about 100-140 m and up to over 1 km, respectively (Jaanusson, 1982). However, my own observations and calculations based on a topographic map indicate a maximum size more or less half the dimension mentioned. The facies is massive pure limestone without obvious bedding, but with frequent open space structures such as stromatactis cavities and synsedimentary dykes. *Ityophorus undulatus* is commonly found with internal sediment in relatively large open space structures. On the rim of these, a unique type of open space structure is often recognised, shown in Figure 2B. Microscopically, internal sediment is dominated by peloids, and the host sediment is micritic (Figure 2D). In case of the Boda Limestone, "normal" stromatactis structures differ considerably both macroscopically and microscopically (Figure 2A, D; or readers are referred to Pratt, 1995, p. 63, fig. 14G). The internal sediment in stromatactis cavities and host sediments of the cavity system is mostly microcrystalline, and peloids are rare. The transversely elongate cavity system with peloids which is similar in construction to that shown in Figures 2B and 2D is generally classified as "zebra cavity of laminoid or flat stromatactis type" (for definition, see Monty, 1995, p. 25), and is interpreted as originating by the decay of superposed thin sheet-like microbial mats (Pratt, 1982).

### Systematic description

The present species was originally described in detail by Warburg (1925, p. 229). General characters and new observations are presented below.

### Genus *Ityophorus* Warburg, 1925

Type species.—*Ityophorus undulatus* Warburg, 1925

### *Ityophorus undulatus* Warburg, 1925

Figure 3

*Ityophorus undulatus* Warburg, 1925, p. 229, pl. 11, figs. 40-43; Moore, 1959, p. O430, fig. 333; Nikolaisen, 1965, p. 237.

**Types.**—3 syntypes, PMU D194 (Warburg, 1925, pl. 11, fig. 40), PMU D195 a, b (Warburg, 1925, pl. 11, fig. 41) and PMU D196 (Warburg 1925, pl. 11, figs. 42, 43), are housed in the Palaeontological Institute, University of Uppsala. PMU D196 is here selected as the lectotype.

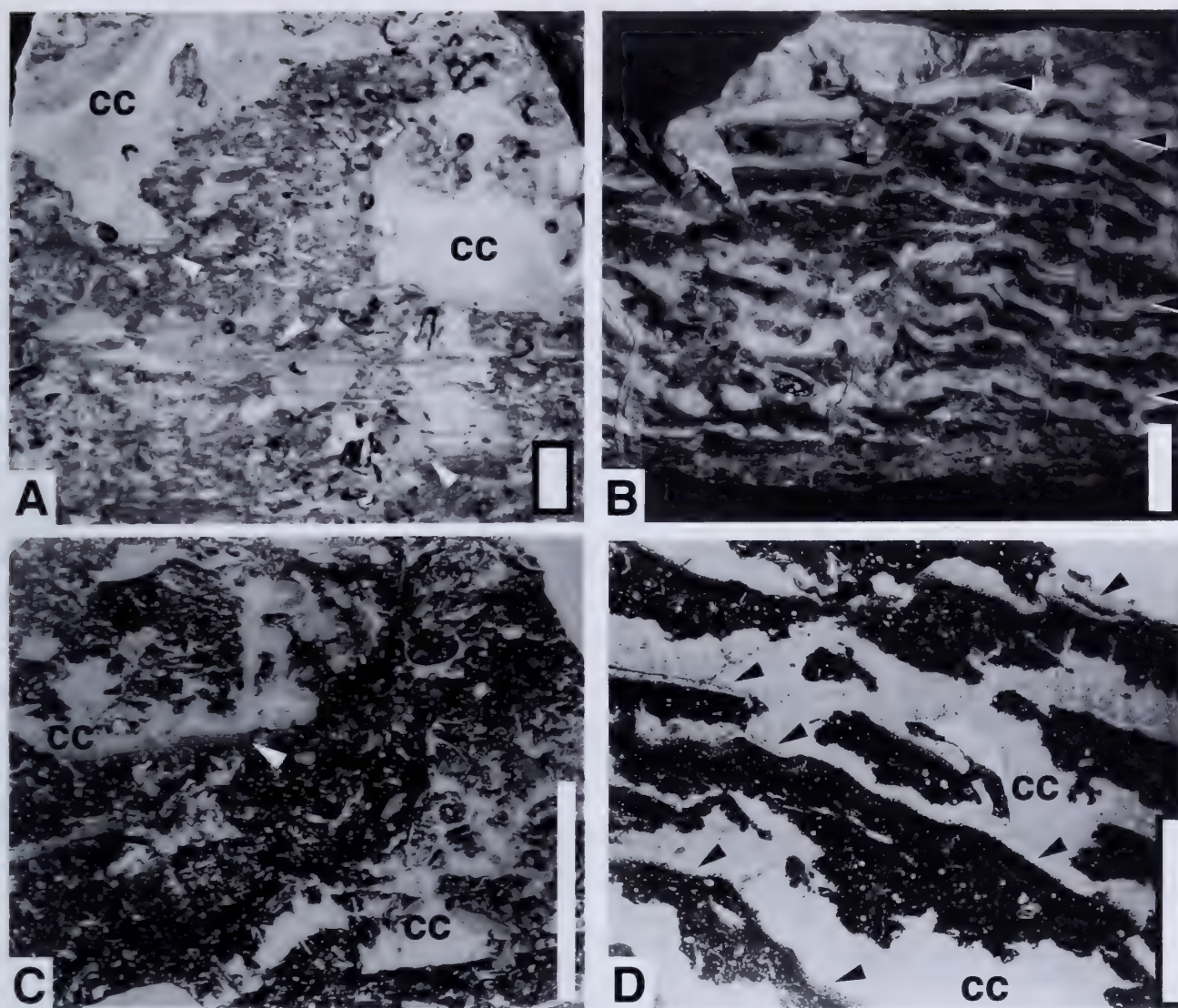
**Type locality.**—Boda Limestone, a buildup mass in Kallholn, Dalarna, Sweden. The stratigraphic level within the mass is unknown. The range of the species is likely to correspond to the Cautleyan to Rawtheyan stage of the Ashgill series, and not the Hirnantian.

**Repository.**—All the specimens figured herein are housed in the Swedish Natural History Museum, Stockholm, with "RM" numbers.

**Description.**—The entire exoskeleton is ovate in outline (Figure 3A). Its entire length seldom exceeds 1 cm. The cephalon occupies about half of the length, sagittally. The axis is fairly convex, and almost half of a circle in cross-section.

The cephalon is horseshoe-shaped (Figure 3A) and strongly convex (Figure 3B). The maximum length including the genal spine is about twice the sagittal length and almost equal to the length of the entire body. The genal angle is acute. The long genal spine curves evenly posteriorly and adaxially. The width of the spine is almost constant throughout. Its posterior end is situated more or less at the level of the posterior end of the pygidium. The anterior cephalic rim, which is narrower and less convex than the posterior cephalic border, disappears where it meets the genal spine. Thus, the genal spine is seemingly an extension of the cephalic posterior border. The glabella is cylindroid in profile and expands slightly anteriorly. It is strongly convex transversely. Three pairs of glabellar furrows are recognised. The 2S and 3S furrows are short and extend more or less transversely. Their length is about one fourth the width of the glabella. The 1S furrow is longer than the 2S and 3S furrows. It is directed about 45° posteriorly from a transverse line. It becomes wider adaxially. Probably the furrow is bifurcated adaxially, but the specimens are too small for a definite observation. The eye ridge is short but strongly convex, and distinctly set off from the surroundings. It extends transversely in front of the level of the 3S glabellar furrows. The length of the eye ridge roughly equals the distance between the 2S



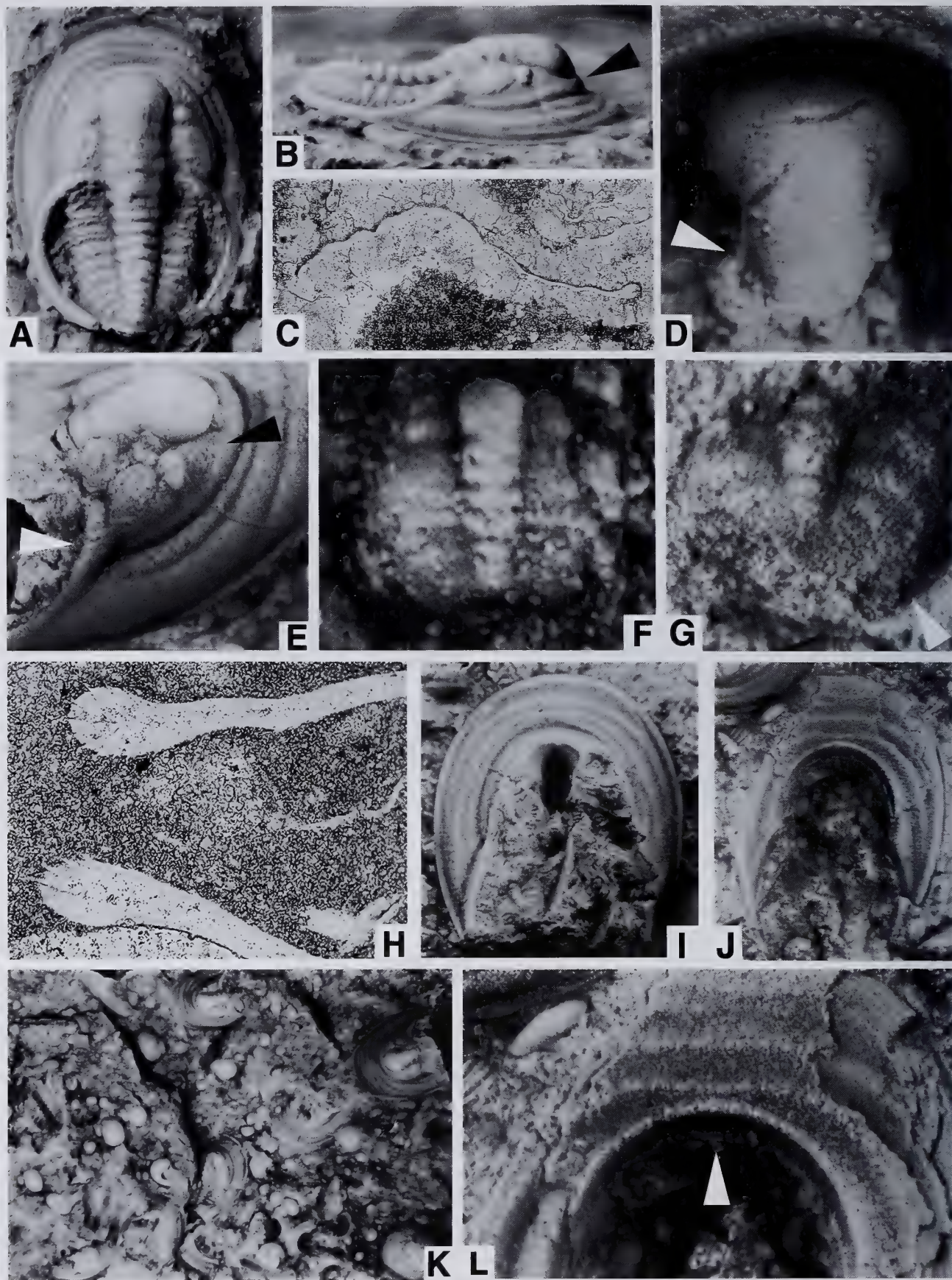


**Figure 2.** Macro- and microfacies of the Boda Limestone. **A.** Polished slab of the core facies, vertical section. White arrows indicate laminated internal sediment. **B.** Polished slab of the "zebra cavity", sampled from the rim of an open space structure. Vertical section. Transversely continued white area pointed by black arrows are cavity systems. **C.** Microfacies of the core facies. Matrix is rich in bioclasts. White arrow indicates microcrystalline internal sediment. **D.** Microfacies of the zebra cavities. Black arrows point to peloidal internal sediment. All white scales are 1 cm. CC stands for cavity filling cement.

and 3S furrow. There may be eyes, as described by Warburg (1925, p. 230). However, the structure described as the eye may be vestigial since it is not proven that there is a visual surface. The possible visual surface forms half a sphere. A median occipital tubercle is present anteriorly on the occipital ring. The peripheral genal area is steeply inclined. Five furrows extend in parallel with the narrow cephalic rim (Figure 3A). The outermost one is the furrow of the cephalic rim. The innermost one extends laterally and posteriorly from the anterior end of the glabella (Figure

3B, E; black arrows). The area between these furrows is moderately convex. The brim, here defined as the area outward of the fourth furrow described above, is broad. The undulating brim has a general dip sagittally from the inner to the outer margin of around 30° (Figure 3C). The dip gradually becomes steeper backwards to about 60° laterally. The facial sutures are of opisthoparian type. Their anterior branches enclose a parabolic anterior part of the cranidium (Figure 3E). The posterior branch extends obliquely backwards to cross the cephalic posterior border







at a right angle (Figure 3E; white arrow). The free cheeks are fused into a single unit, because no furrows or gaps are recognised on the cephalic doublure (compare dorsal and ventral cephalic views in Figure 3I, J, respectively). The doublure closely follows the shape of the brim, and the space between the two is very narrow (Figure 3C). The doublure is wide (Figure 3C, J, L). The interior edge of the doublure (Figure 3L; white arrow) is situated below the innermost parabolic furrow in the cephalon, which is indicated by black arrows in Figure 3B, E. The cephalic doublure has three or four parabolic furrows which are almost parallel to the cephalic margin (Figure 3J). An interior part of the doublure, between the fourth and fifth parabolic furrow mentioned above, is steeply inclined and distinctly set off from the surrounding. Thus the cephalic doublural morphology is quite similar to the lower lamella of harpids.

In the cephalic rim, terrace lines with an asymmetrical cross-section are recognised on both the dorsal and ventral side (Figure 3H). The steep surfaces of the ventral terrace lines face dorsally, whereas they face ventrally in the dorsal ones (for detail, see Figure 5).

The hypostome is situated just below the glabella (Figure 3I). Its anterior margin must have been in contact with the cephalic doublure mesially. Three specimens among hundreds of cephalons show the same position of the hypostome. Thus the described position of the hypostome should be original. The length of the hypostome is 55% of that of the glabella (Figure 3D). It is strongly convex transversely. The maximum length is about 1.3 times longer than the maximum width. An anterior wing is relatively long (exsag.) and evenly inclined dorsally. The distal part of the wing is broadly rounded. The anterior margin is slightly depressed medially. The lateral border is narrow and short. The border furrow extends from the level of the posterior end of the anterior wing to four-fifths of the anterior end of the hypostome. The shoulder is triangular in shape and horizontally extended (Figure 3D; white arrow). The posterolateral corner of the central body is angulate. The posterior margin is convex without a border. No distinct boundary separating the anterior and the posterior lobes is recognised. The central body is longitudinally elliptic in shape.

The thorax consists of six segments (Figure 3A). The axis gradually becomes narrower backwards. The ratio between axial and pleural widths ranges from 1 to 1.2 from in front to the rear. The pleurae extend almost straight transversely except for the posteriormost two segments, in which the pleurae distal to the geniculation curve moderately backwards. A distinct pleural furrow is present. It extends almost parallel to the anterior and posterior margins of the segment.

The pygidium is wide (Figure 3A). The maximum width/length ratio is about 1.9. Six axial rings and five pairs of pleural ribs are discernible. Distal to the fulcrum, pleural ribs and furrows curve gently backward. Pleural and interpleural furrows lie parallel with each other. The posterior end of the axis is obscure. It gradually dies out posteriorly. A narrow flattened border is present.

Specimens of a younger growth stage, a meraspid degree? (Figure 3F), and a transitory pygidium (Figure 3G) are available. Both specimens are found along with adult specimens in internal sediment. No other trilobite species is recognised in this sediment. The former specimen (Figure 3F) is most probably a moult, because it lacks the entire free cheek unit. The glabella is proportionally narrower than in the adult. The 2S furrow differs in its course from that of the adult. The abaxial end of the furrow does not reach to the axial furrow. The furrow is directed posteriorly and adaxially in the young specimen, but transversely in adults. The axial ring of the first thoracic segment is seen posterior to the cephalon. A distinct eye ridge is present. Its proportion and position in relation to the glabella is almost the same as in an adult specimen. A most notable feature is the facial suture course. The anterior branch is not parabolic as in adult specimens, but extends straight forwards. The transitory pygidium seems to have a spiny margin (Figure 3G; white arrow). The posterior extremity of the axis ends well in front of the margin. The preservation is not good enough to permit further observations.

*Remarks.*—Previously, Warburg (1925, p. 231) described the genal spine of the present species as being a short pointed spine. Because of the minute size of the species, it tends to be broken. In most of the cases the genal spine is recognised as a concave mould.

◀ **Figure 3.** *Ityophorus undulatus* Warburg, 1925. **A.** Complete exoskeleton, dorsal view.  $\times 18$ . Jutjärn. RM Ar 56890. **B.** Same, lateral view.  $\times 17$ . Black arrow points to the furrow, below which the inward edge of the doublure is situated. **C.** Exsagittal or sagittal section of the cephalon.  $\times 39$ . Jutjärn. RM Ar 56891. **D.** Hypostome, ventral view.  $\times 54$ . Jutjärn. RM Ar 56892. White arrow points to the posterior wing, which is partly broken. **E.** Cephalon, oblique lateral view showing curving facial suture course.  $\times 15$ . Locality unknown. RM Ar 56893. White arrow points to the termination of the posterior branch of the facial suture. Black arrow to the furrow, below which the inward edge of the doublure is situated. **F.** Fairly young individual.  $\times 70$ . Jutjärn. RM Ar 56894. **G.** Fairly young pygidium.  $\times 65$ . Jutjärn. RM Ar 56895. White arrow points to pygidial spine. **H.** Magnified brim in cross section.  $\times 150$ . The lower brim of the two is upside down. Jutjärn. RM Ar 56896. **I.** Ventral mould of hypostome and cephalic brim, dorsal view.  $\times 16$ . Specimen is in the same slab as G. **J.** Cephalic doublure, ventral view.  $\times 12$ . Same slab as E. **K.** Occurrence pattern with microgastropods.  $\times 4$ . Same slab as E. **L.** Magnified cephalic doublure, ventral view.  $\times 45$ . Specimen same as J. White arrow points to the inner edge of the cephalic doublure.



### Systematic position of *Ityophorus undulatus*

#### Morphological characters of *Ityophorus* and *Frognaspis*

For more than a half century, opinion on the high-rank classification of the present genus was far from a clear consensus. First, Warburg (1925) made a new family Ityophoridae consisting of only the present genus. Later in Moore (1959), the species was doubtfully classified as a member of the Trinucleina Swinnerton, 1915, of the order Ptychopariida without any demonstrated evidence. It is clear that the convex cephalon with horseshoe outline is just a superficially similar to a trinucleid cephalon. Nikolaisen (1965) described a new species, *Frognaspis stoermeri*, which is closely related to the present species, from the Middle Ordovician of Norway, and classified it into the Ityophoridae. Furthermore, he implied a neotenic development of the present species from *Frognaspis stoermeri*. As will be discussed in a later paragraph, *Frognaspis stoermeri* shares fairly many characters with the present species. The suggestion of a close relationship between the two is therefore convincing. However, Nikolaisen did not tackle the problem of the position of Ityophoridae. Fortey (1997) also gave up and simply stated that the family belongs to the Ptychopariida Swinnerton, 1915.

Before examining the high-rank systematic position of the present species, we must understand how the unique morphology evolved in the phyletic lineage. Since *Ityophorus undulatus* preserves characters seen in young individuals of *Frognaspis stoermeri*, the heterochronic evolution of the former from the latter is worth consideration. After comparison of the two, we can sort out a "heterochronic polish". Then we can define stable characters and infer the ancestral conditions of characters which differ between the two. In addition, one has to remember what kind of morphological changes would arise in a shift to cavity-dwelling habits in modern arthropods.

Characters shared between *Ityophorus undulatus* and *Frognaspis stoermeri* are as follows:

- 1) wide cephalic brim.
- 2) facial suture course.
- 3) distinct furrows in the cephalic doublure.
- 4) small eyes.
- 5) fairly wide cephalic doublure with distinct narrow cephalic rim.
- 6) free cheeks forming single unit.
- 7) distinct pleural furrow (known only from the pygidium in the latter species).
- 8) narrow flattened pygidial rim.
- 9) pygidial pleural ribs distal to the geniculation extend obliquely backwards.
- 10) hypostomal morphology.
- 11) directions of pleural tips in the thorax.

- 12) cephalic doublural margin smoothly rounded mesially (no embayment for the hypostomal suture). Since the mesial part of the inner margin of the doublure is below the anterior extremity of the glabella, the hypostome should be attached to the doublure medially.

Characters which are not shared by the two species are:

- 1) glabellar profiles (expanded in *Ityophorus*).
- 2) glabellar furrows (deepened adaxially and 1S furrows faintly connected over midline in *Frognaspis*).
- 3) number of segments in the pygidium.
- 4) ornaments on dorsal surfaces.

The characters 1) and 2) in *Ityophorus* are apparently derived from younger growth stages of *Frognaspis* (see Nikolaisen, 1965, pl. 3, fig. 4). The inferred ancestral conditions of the two characters should thus be represented in the adult stages of *Frognaspis*.

The ancestral glabellar character 1) should be preserved in the adult stage of *Frognaspis*. This is because the glabellar profile in *Ityophorus* is fairly similar to a younger stage of *Frognaspis* (Nikolaisen, 1965, p. 243). Thus the ancestral group should have had an anteriorly tapering glabella, and possibly the 1S furrows may have been connected mesially (non shared character 2). The latter situation is recognised in *Frognaspis*.

Determining the ancestral condition of character 3) is difficult. This is because the adult number of pygidial segments is, in general, related to the number of thoracic segments. Unfortunately, the exact number of thoracic segments is not known in *Frognaspis*. I can only say that the ancestral condition of the number of segments in the pygidium may vary between species in the high-rank group, in which the two species belong.

Concerning character 4), since the exoskeletal ornament pattern is unstable among the genera in some family groups (e.g., Styginidae), we should hesitate to use that character in determining the high-rank systematic position. In general, recent cavity-dwelling organisms are equipped with specialized sensory organs. Especially in cavity-dwelling arthropods, the appendages tend to be long, which increases the area for the number or the size of sense organs (Culver, 1982, p. 17). Coarse tubercles on the exoskeletal surface in trilobites are generally understood as sensory ducts (Osmólska, 1975, p. 203). As will be discussed in a later paragraph, *Ityophorus* must have had long appendages, so the animal had the potential to equip its appendages rather than the dorsal exoskeleton richly with sensory organs. Thus smoothing of the dorsal exoskeletal surface may be a result of adaptation inhabiting cavities.

#### Discussion of systematic position of *Ityophorus*

I first try to narrow down candidate ancestral groups of *Ityophorus* from other groups with yoked free cheeks.



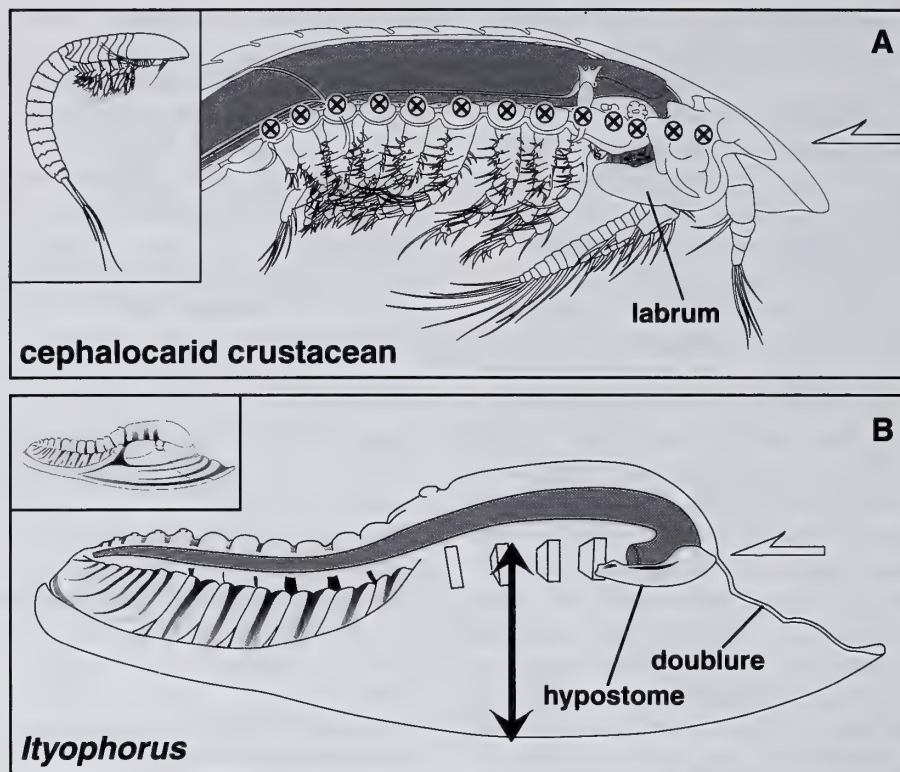
Next, I judge the possible relationships based on other characters such as ventral morphology, facial suture type, and pygidial morphology.

Trilobite groups which possess yoked free cheeks are bathynotids and conocoryphids from the Lower to Middle Cambrian, Nileidae, Phacopida, Trinucleina, Harpina, Olenidae, Hypermecaspididae, some species of Dikelocephalidae such as *Dikelocephalus retrorsus*, Loganellidae, some species of Dikelocephalinidae (readers are referred to *Dactylocephalus latus* (Peng, 1990a, pl. 9, fig. 8) and *Ciliocephalus angulatus* (Peng, 1990b, pl. 17, fig. 3)), Harpididae and Entomaspididae. Of these, the Lower Cambrian groups are so different in several characters such as facial suture courses, pygidial morphology and ventral cephalic characters, that a phylogenetic relationship with *Ityophorus* or *Frognaspis* is most unlikely. Harpina and conocoryphids (marginal suture), Harpididae (marginal or characteristic proparian suture), Phacopida (proparian suture) are profoundly different in their facial suture types from that of *Ityophorus*. Among the rest, the Entomaspididae have a characteristic pygidial morphology (a narrow upturned (geniculated) border or stubby spines in front of a continuous pygidial rim: Ludvigsen *et al.* 1989, p. 47) which is unlikely of the ancestor of *Ityophorus*. Most of the Trinucleina do not have eyes with dorsal facial suture except some genera such as *Orometopus* which has opisthoparian facial sutures. However, the overall morphology, especially the pygidial morphology of trinucleid type is quite different from the *Ityophorus* pygidium with distinct border and posteriorly curved pleural and interpleural furrows. The Nileidae have a characteristic hypostome, cephalic and pygidial morphology, large eyes with no eye ridges, more or less straight pygidial furrows, all of which are unlikely in a relative of *Ityophorus*. The Olenidae and the Hypermecaspididae have yoked free cheeks. In the case of olenids and hypermecaspidids with a wide preglabellar field, the cranidium is similar in outline and the cephalic doublural margin smoothly rounded mesially as in *Ityophorus*, but the hypostomes become natant. Since the hypostome of *Ityophorus* and *Frognaspis* must have attached mesially to the cephalic doublural margin (shared character 12), their ancestor should have possessed this mode of hypostomal attachment. Moreover, the pleural and interpleural pygidial furrows of the Olenidae and the Hypermecaspididae extend obliquely posteriorly in a more or less straight way, which is different from the situation in *Ityophorus*. Therefore, a phylogenetic relationship between the Olenidae and *Ityophorus* is unlikely.

Other candidates are the Dikelocephalidae, Dikelocephalinidae and Loganellidae. Some species of the former two families, although not all, possess yoked free cheeks with a wide cephalic doublure. The pygidial morphology is also

fairly similar between them. The Dikelocephalidae and the Loganellidae were extinct before the Cambrian-Ordovician transition, whereas the Dikelocephalinidae persisted beyond that boundary (Öpik, 1967, p. 254). One could therefore think that the third group, the Dikelocephalinidae, might contain the ancestor of *Ityophorus*. Classifying the Dikelocephalinidae is usually difficult, because most of the characters are too general to be diagnostic (Fortey and Chatterton, 1988, p. 209). However, the pygidium of Dikelocephalinidae has posteriorly curved pleural furrows but not interpleural furrows whereas *Ityophorus* has both. Thus, Dikelocephalinidae should not be related to *Ityophorus*. The Dikelocephalidae and the Loganellidae have interpleural furrows in their pygidia. However in the former, an embayment is present mesially in the cephalic doublure for an attachment of the hypostome. In contrast, the Loganellidae have a mesially smooth outline of the cephalic doublure (Moore, 1959, p. O333) which is concordant with the ventral cephalic morphology in *Ityophorus*. Below I discuss the phylogenetic relations between the Loganellidae, and *Ityophorus* and *Frognaspis*.

There are several shared characters between the Loganellidae and the two species such as the shared characters between *Ityophorus* and *Frognaspis* 1), 2), 5), 6), 7), 8), 9) and 11) listed above. Furthermore the characters of the inferred ancestral conditions which are listed as non-shared characters between *Ityophorus* and *Frognaspis* 1) and 2) fit well to this family. Generally, in species with the free cheeks in a single unit and a wide doublure, the cephalic rim [called a "border" in Fortey and Chatterton 1998: fig. 6, readers are referred to Whittington and Kelly (1997, p. 315) for the terminology of the "border" and "rim"] is of fairly low convexity (e.g., Fortey and Chatterton, 1988, fig. 6). Nikolaisen (1965, p. 237) stressed the differences in eye size and the hypostomal morphology in species between loganellids and *Frognaspis* or *Ityophorus*, but the reduction of eye size is a common feature in organisms adapted to cavities (Humphreys, 2000, p. 4). Anteriorly in the hypostome of *Ityophorus* and *Frognaspis*, there is a unique longitudinal median groove (Figure 3D; Nikolaisen, 1965, pl. 3, fig. 6). The groove structurally corresponds to the median longitudinal groove or depression (see Nikolaisen, 1965, pl. 2, figs. 1, 3; pl. 3, figs. 1, 2) anteriorly in the *Frognaspis* glabella. In general, species with yoked free cheeks (e.g., *Cloacaspis senilis*; see Fortey, 1974, pl. 10, fig. 6) may or may not possess a similar longitudinal glabellar groove or depression. If present, the longitudinal groove in the glabella tends to be more weakly impressed in older growth stages (Fortey, 1974, fig. 6). Thus the groove is more or less an embryonic character. Hence the two latter genera are most likely descended from a species of the Loganellidae. However, there are still several facts



**Figure 4.** A. Schematic drawing of cephalocarid crustacean showing the structural relationship in basal appendage joints (represented as "X" in a circle), digestive tract (grey area), labrum and basal podomere. Positions of the joints are situated above the level of the mouth opening. Modified from Sanders (1963: fig. 4) and Hessler and Elofsson (1992: fig. 3). B. Schematic drawing of *Ityophorus undulatus* showing structural relationship in inferred digestive tract (grey tube), hypostome and basal podomeres (represented as bricks). White arrows indicate dorsoventral level of mouth openings. Black double arrow indicates minimum distance between basal joints of appendages and the substrate.

which may differentiate *Ityophorus* and *Frognaspis* from typical Cambrian loganellids: 1) the two are Middle to Late Ordovician trilobites, 2) the body size of the two has undergone considerable shrinking, 3) the presence of crescentic furrows in the doublure (shared character 3) in the two species, but not in Cambrian loganellids. Therefore, the two genera are best accounted for as a subfamilial group of the Cambrian Loganellidae. *Ityophoridae* Warburg, 1925, including *Frognaspis* and *Ityophorus*, is therefore downgraded to a subfamily *Ityophorinae* Warburg, 1925, of the family Loganellidae Rasetti, 1959.

The *Ityophorinae* now appears to be a relict of the Late Cambrian group. Since growth stages are unknown in most fossil arthropods, how the *Ityophorinae* had evolved from a loganellidae as becomes vague. Recent animals, "progenetic evolution" is quite common as part of a cryptic adaptation, and the considerable size decrease of the *Ityophorinae* in comparison with the Loganellidae may be one indication of "progenetic evolution".

### Functional morphology of *Ityophorus undulatus*

The present species had attained a body with apparently a "snow-shoe" effect, which increases the area of the animal substrate interface and prevents the animal from sinking into the substrate. A parallel is seen in harpid trilobites, although previous functional studies of these were restricted to the function of their characteristic brim. Unfortunately, we have no data on appendages in *Ityophorus* or harpid trilobites. It may be worth trying to infer the length and use of the legs from the space relationships between the probable attachment of the legs and the head shield, particularly its margin. This may give some hint of the mode of life.

### Elevation of leg insertion over substrate

The hypostome of *Ityophorus* is oriented horizontally (Figures 3I, 4). This means that the mouth opened backwards, and not downwards. Recent crustaceans such as cephalocarids and notostracans a structure similar to the trilobite hypostome plus associated soft tissue is present, al-



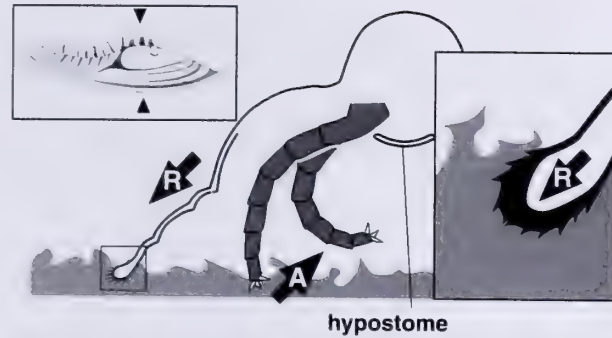
though it is not homologous. This is the “labrum”. In a crustacean with a labrum the digestive tract first extends forwards from the mouth. The tract then flexes in the head and continues backwards (Figure 4; see grey area in the cephalocarid), extending more or less straight to the anus. The digestive tract in *Ityophorus* should have followed the same course as in the cephalocarid crustacean (Figure 4; *Ityophorus* with digestive tube in grey). Actual evidence on such a digestive course in trilobites is reported in phacopid (Stürmer and Bergström, 1973, pl. 20) and trinucleid trilobites (Šnadjr, 1987, fig. 3).

In case of a crustacean with the mouth opening backward, there is an important structural relationship between the dorsoventral positions between the labrum and the basal podomeres. Since the mouth is directed backwards, food particles have to be transported mechanically (handled by appendages) or indirectly (handled by food collecting wave created by appendages) from back to front *via* the midventral line. For transporting the food particles, the “labrum” and mouth must be situated below the level of the midventral line posterior to the labrum. Since the line is higher than the labrum and the mouth, the basal podomeres, which are attached to the axial body, automatically are at more or less the same horizontal level as the mouth opening. Such a relationship is seen in three-dimensionally preserved *Ceraurus* (Walcott, 1881, pl. 2, figs. 1–3). In *Ityophorus*, the spatial relationship between hypostome and basal podomeres appears to have been identical (see white arrow in Figure 4B). Therefore, the basal podomeres must have been situated fairly high relative to the cephalic margin (Figure 4). This configuration forced the animal to develop long appendages simply to reach the substrate. As discussed earlier, this condition is a common feature in cavity-dwelling arthropods, and *Ityophorus* could probably rest with the brim on the substrate without using its appendages. This means that the appendages were free to be used for different aims such as food collecting.

#### Relationship between brim and appendages

In general, the morphology of the arthropod appendages directly influences the method of feeding. The combination in *Ityophorus* of long legs surrounded by a brim forming a long “skirt” should have been of significance for the mode of life. As described above, the two sets of terrace lines are restricted to the edge of the brim, where the steep sides of each set face the other set (Figures 3H, 5). The lower set of terrace lines should have prevented the animal from sliding laterally outwards (Schmalfuss, 1981), while the inner set would hinder extensive sinking into the substrate.

When an appendage scratched the substrate in one direction (Figure 5; black arrow with A), the body would be subjected to a pull in the opposite direction (Figure 5; black



**Figure 5.** Schematic drawing of transversely sectioned cephalon (black arrow in top of the figure) with inferred appendage, showing the relationship of the action and reaction mechanics between the exoskeleton and the substrate when the animal was scratching. The rectangle shown in the right of the figure is the magnified cephalic rim with substrate. For more details, see text. Black arrow with A means the vector of action from exoskeleton to the substrate, black arrow with R of reaction from the latter to the former.

arrow with R). This is determined by simple physical rules. Scratching or burrowing leg movements may also tend to pull animal downwards into the substrate. In *Ityophorus*, the terrace lines on the cephalic rim would hinder the head shield from sliding sideways or downwards (Figure 5; see magnification in left rectangle). Thus, for as long as the animal kept scratching, it could presumably move along inclined walls in a cavity. This mode of behaviour would work on a gel-like or sticky substrate such as a bacterial mat, the existence of which is suggested by the geological setting. Such a mode of life must require one more important factor, a low weight of the animal. *Ityophorus* was indeed unusually small and light. Therefore, I conclude that *Ityophorus* was most probably adapted to cavities coated with microbial mats. Some examples are known from Recent cavity-dwelling arthropods such as isopods which feed directly on fungi and bacteria (Sarbu and Popa, 1992).

#### Epilogue

The Late Ordovician trilobite *Ityophorus undulatus* appears to have had a set of morphological characters characteristic of cavity dwellers, such as reduced eyes, long appendages relative to the body length, considerable dwarfing, and possible heterochronic development, which is most likely to be progenesis. The supposed ancestral group of the Ityophorinae, the Loganellidae, is thought to be extinct before the Cambrian-Ordovician transition. A relict group might have persisted into the Ordovician by “progenetic evolution”, and later adapted into a cryptic life. This is the first report that tries to interpret a phylogenetically relict fossil group as cryptic animals.



A Devonian proetid genus, *Denemarkia* (see Moore, 1959, O397; Snajdr 1980, p. 146, pl. 37), was a possible cavity dweller (Alberti, 1969, p. 336) with an overall morphology similar to *Ityophorus*. Taphonomical evidence showing the entombment of *Denemarkia* specimens in a cavity is available (such an occurrence pattern is not illustrated so far but a slab showing such a situation is stored in National Museum, Czech Republic, museum number L 16634). *Denemarkia* is known from the Devonian Koněprusy Limestone in Czech Republic (Šnajdr, 1980) and the Kess Kess Limestone in Morocco (Alberti, 1969). Both limestone units are of the carbonate mud mound type of buildups. Interestingly, shared characters between *Denemarkia* and *Ityophorus*, such as fairly vaulted cephalon (see Moore, 1959, fig. 302-1b), distinct cephalic rim with wide cephalic doublure, lacking mesial embayment for the hypostomal suture (see Snajdr, 1980, pl. 27, fig. 9), a combination of which is quite rare in proetids, and less developed eye, are a fairly unique morphological combination in trilobites. A major morphological difference between the two is that the dorsal exoskeleton of *Denemarkia* is fairly rich in tubercles, whereas *Ityophorus* is smooth, and this can be explained as a result of adaptation to cavities as discussed previously. Repeated body modifications into ityophorid-like morphology from completely different clades means that there was a general capacity in the Trilobita to evolve in this direction.

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# Changes in Holocene ostracode faunas and depositional environments in the Kitan Strait, southwestern Japan

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**Abstract.** At least 106 species were identified from 36 samples obtained from two cores (T1 and T2), which were recovered from the Kitan Strait off Wakayama City, southwestern Japan. Q-mode cluster analysis of cores T1 and T2 revealed three biofacies (PL, PT and LS). Changes in depositional environments based on the observed distribution of ostracodes were analysed, and the following sequence is proposed. Before ca. 7,000 cal yr BP, the T1 site was a sandy coast, ranging from an outer bay to the open sea, close to a river mouth, at water depths of more than 15–20 m, while the T2 site ranged from a bay coast to an outer bay, close to a river mouth, at water depths of less than 15–20 m. During ca. 7,000–2,000 cal yr BP, the position of the sites fell within ranging an outer bay to the open sea at water depths of 30–40 m influenced by residual and/or tidal currents from the straits. After ca. 2,000 cal yr BP, the sites were situated on a sandy coast, ranging from an outer bay to the open sea, close to a river mouth, at water depths of more than 15–20 m. Two new species, *Trachyleberis ishizakii* and *Cytheropteron kumaii*, are also described.

**Key words:** depositional environments, Holocene, Kitan Strait, Ostracoda, Wakayama

## Introduction

Fossil ostracodes have frequently been used to elucidate the way in which the environment of deposition changes with time (e.g., Ishizaki *et al.*, 1993; Cronin *et al.*, 1994; Irizuki *et al.*, 1998b), because they are highly sensitive indicators of several environmental factors (e.g., Ishizaki and Irizuki, 1990; Ikeya and Suzuki, 1992; Yamane, 1998; Yasuhara and Irizuki, 2001). However, little studies of Japanese Holocene ostracodes have been carried out (Frydl, 1982; Ishizaki, 1984; Ota *et al.*, 1985; Ikeya *et al.*, 1987; Ikeya *et al.*, 1990; Iwasaki, 1992; Kamiya and Nakagawa, 1993; Irizuki *et al.*, 1998a; Miyahara *et al.*, 1999; Irizuki *et al.*, 2001). Many of these studies concentrate on temporal changes of Holocene ostracode assemblages in small drowned valleys and enclosed bays. Irizuki *et al.* (1998a) elucidated paleoenvironmental changes on the western coast of the Miura Peninsula, central Japan on the basis of numerical analyses of ostracode distributions. Miyahara *et al.* (1999) and Irizuki *et al.* (2001) used sedimentary facies

from cores, containing fossil ostracodes and high density radiocarbon dating to construct a relative sea-level curve and to discuss paleoceanic changes in the Osaka area, southwestern Japan.

The Kitan Strait is situated between Osaka Bay and the open sea. The area provides an important record of the depositional environments of the Seto Inland Sea and Osaka Bay, and therefore yields key data for inferring paleoceanic conditions.

This study aimed to elucidate ostracode faunas and the temporal change in depositional environments off the western coast of Wakayama City, near the Kitan Strait. We also discuss the consequences of sea-level changes in Osaka Bay and the study area.

## Locality, lithofacies and methodology

Drilling cores (T1 and T2) were excavated by the National Institute of Advanced Industrial Science and Technology from the Kitan Strait (T1: 34°14.7' N, 135°5.2' E, 19.61 m

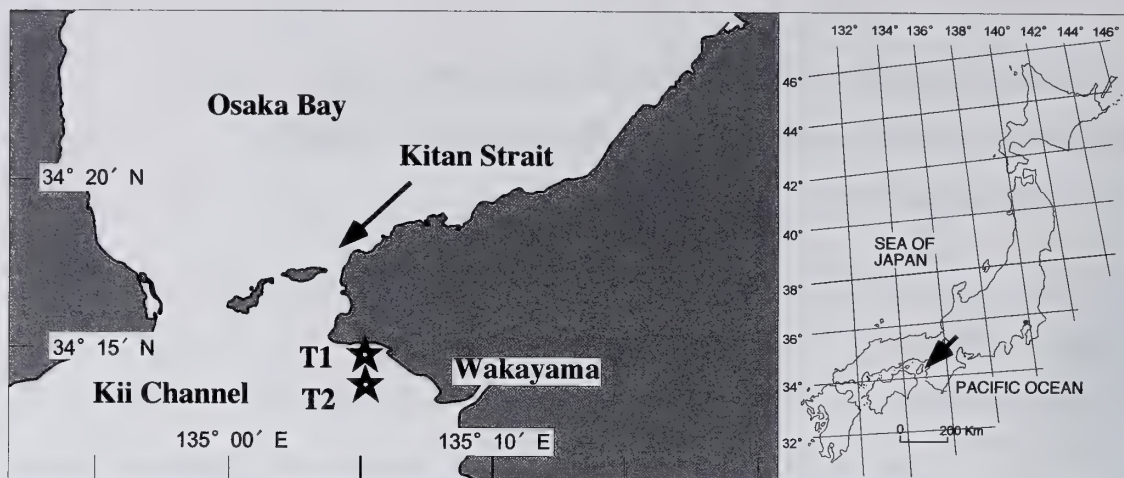


Figure 1. Index and locality maps.

water depth; T2: 34°14.5' N, 135°5.2' E, 24.78 m water depth) off Wakayama City, southwestern Japan (Figure 1). Nanayama *et al.* (1999) described in detail the Holocene and upper Pleistocene sequences in cores T1 and T2. We briefly mention those sequences here (Figure 2). Sediments at altitudes lower than -33.5 m in core T1 and -38.3 m in core T2 consist of sand and gravel, and the enclosing matrix is coarse sand. Sediments at altitudes between -19.6 and -33.5 m in core T1 and between -24.8 and -38.3 m in core T2 consist of alternating beds of fine to medium sand layers and silt layers with shell fragments, showing intensive bioturbation. Nanayama *et al.* (1999) reported two layers of debris flow deposits (Df1 and Df2). Df1 is situated at altitudes of approximately -24.1 to -24.3 m in core T1 and -29.3 to -30.4 m in core T2 (Figure 2). Df2 is situated at altitudes of approximately -27.2 to -27.7 m in core T1 and -34.5 to -35.7 m in the core T2 (Figure 2). Volcanic glasses are concentrated at an altitude of approximately -31 m in core T2. Nanayama *et al.* (1999) reported that these volcanic glasses are correlated with the Kikai-Akahoya (K-Ah) volcanic ash, dated at ca. 7,300 cal yr BP (Fukusawa, 1995).

Samples of the sediment core, each approximately 5 cm thick, were immersed in water, boiled for about one hour on a hot plate, washed through a 75  $\mu$ m sieve and then dried. Dry weights were calculated from the original sample weight, scaled by the percentage water content of each sample. The fraction coarser than 200  $\mu$ m was sieved to allow the ostracode fauna to be determined, and for specimens of each taxon to be obtained. Samples containing abundant ostracode specimens were divided using a sample splitter into workable aliquots of approximately 100–200 specimens. In the remaining samples, all the specimens present were picked. The number of specimens refers to

the estimated minimum number of carapaces present in each sample, determined by taking the total number of left or right valves, whichever was the greater.

### Ostracode biofacies

At least 106 ostracode species were identified from 36 samples obtained from cores T1 and T2 (Appendix). A selection of these species is illustrated in Figure 3.

Q-mode cluster analysis was used to examine vertical changes in ostracode faunas and to determine ostracode biofacies, which would closely reflect variations in the depositional environment. Taxa represented by three or more specimens in any one sample were used for analysis (some *Aurila* and *Pontocythere* species groups are expressed collectively as "spp."), and each sample contained more than 50 specimens. Horn's overlap indices (Horn, 1966) were used to assess similarities, and clustering was achieved by the unweighted pair-group arithmetic average method. The results revealed three biofacies (PL, PT and LS; Figure 4). To interpret these biofacies reflecting depositional environments, we referred to the distributions of present-day dead ostracode shells, because many studies of the distributions of present-day ostracodes have been based on dead ostracode shells.

Figures 5 and 6 show the stratigraphic positions of biofacies and percentages of 24 taxa dominating each of the biofacies in these cores.

(1) *Biofacies LS* (*Loxoconcha viva*-*Spinileberis quadriculeata* biofacies).—Biofacies LS is composed of seven samples and lies in the middle part of cores T1 and T2. It is characterized by the dominance of *Loxoconcha viva* Ishizaki, *Spinileberis quadriculeata* (Brady) and *Cytheropteron kumaii* sp. nov. (= *Cytheropteron miurense* of Ikeya



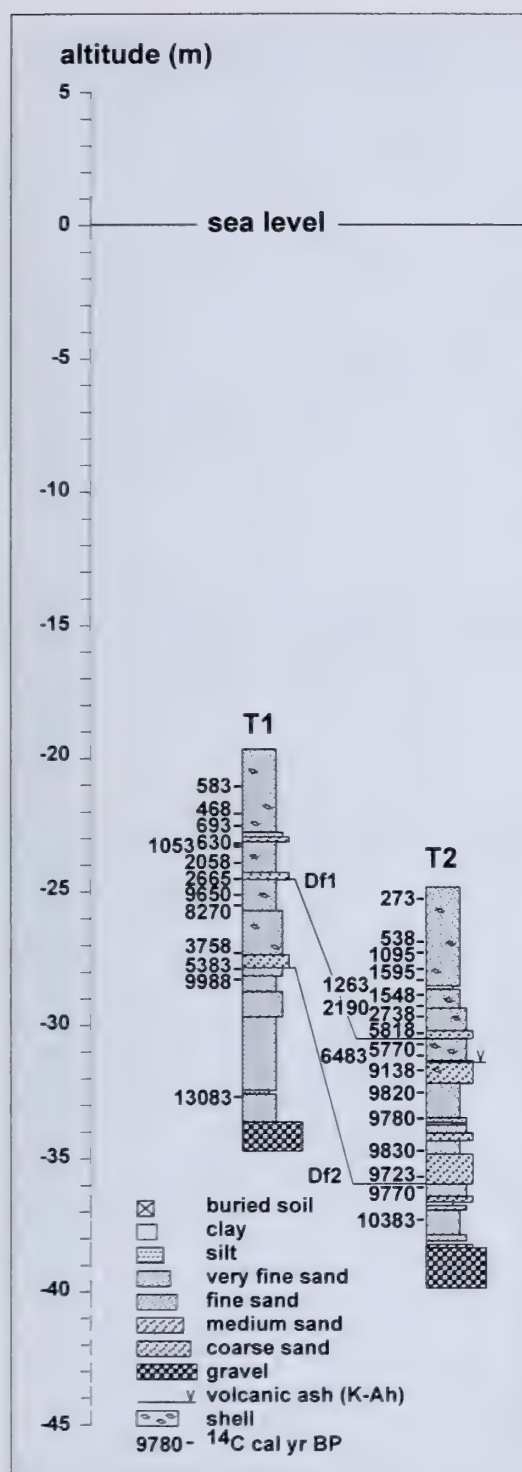


Figure 2. Columnar sections of T1 and T2 cores and horizons of radiocarbon age (cal yr BP). Radiocarbon ages calibrated and columnar sections modified from Nanayama *et al.* (1999).

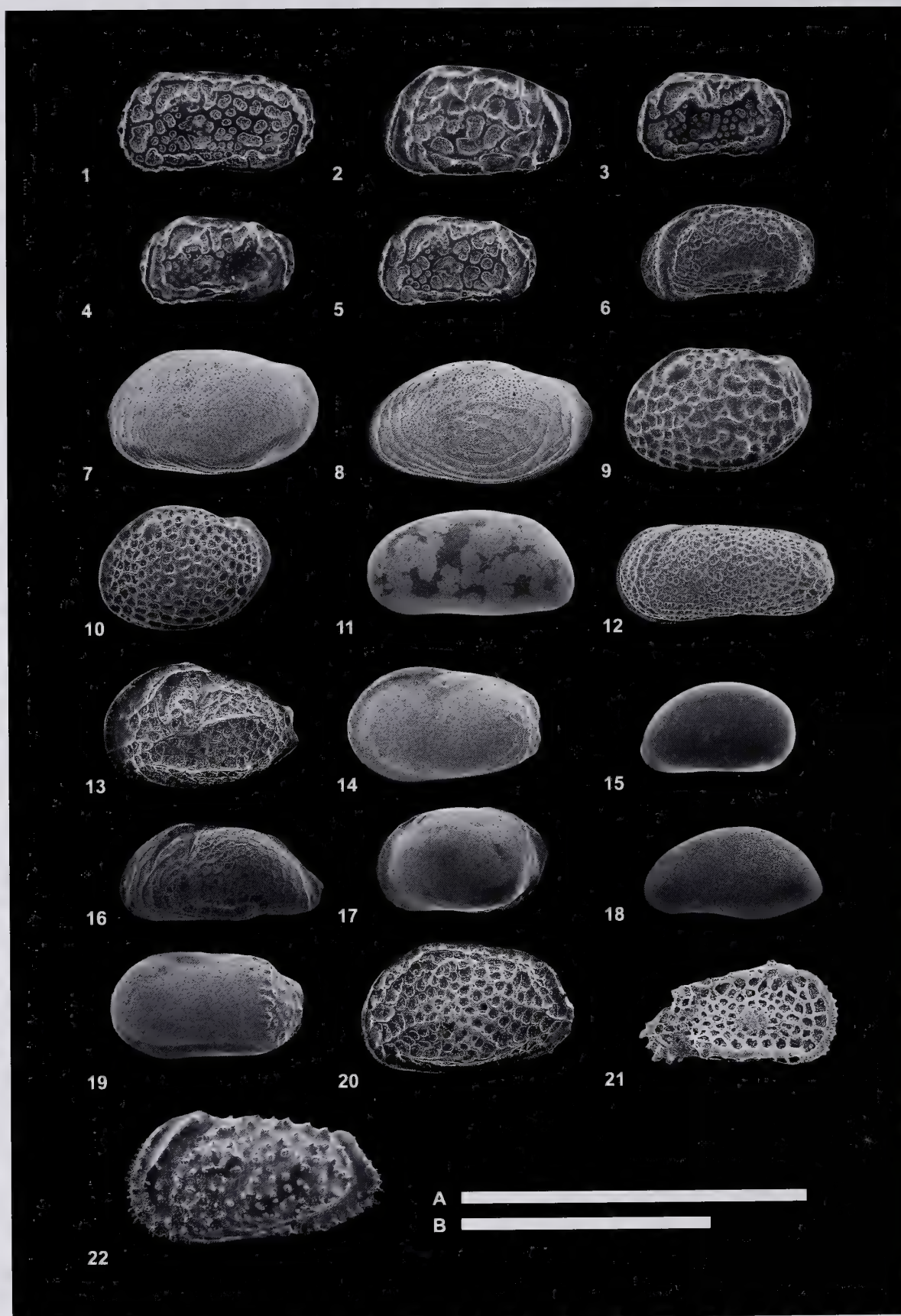
and Itoh, 1991 and *Cytheropteron* sp. of Yasuhara and Irizuki, 2001). *Ambtonia obai* (Ishizaki), *Falsobuntonia hayamii* (Tabuki), "form A" (Abe and Choe, 1988) of *Bicornucythere bisanensis* (Okubo), *Aurila spinifera* Schornikov and Tsareva s.l., *Krithe japonica* Ishizaki, *Kobayashiina donghaiensis* Zhao and *Amphileberis nipponica* (Yajima) are also common.

*L. viva* is abundant at water depths of 15–37 m in Tateyama Bay, central Japan (Frydl, 1982). *S. quadriaculeata* is common in most areas of Osaka Bay and Hiuchinada Bay (Yasuhara and Irizuki, 2001; Yamane 1998). *C. kumaii* is reported from the outer part of Sendai Bay near the open sea at water depths of more than 50 m (Ikeya and Itoh, 1991) and from Osaka Bay at water depths of 37.2 m (Yasuhara and Irizuki, 2001). *Falsobuntonia* (*hayamii* and *taiwanica* Malz) is commonly found in the open sea off Shimane at water depths of more than 50 m (Ikeya and Suzuki, 1992). *A. obai* is abundant at water depths of 20–40 m (e.g., Ishizaki, 1971; Frydl, 1982; Bodergat and Ikeya, 1988). *A. spinifera* s.l. is reported from the sandy part of Hiuchi-nada Bay near the Kurushima Strait (Yamane, 1998) and from the sandy part of Osaka Bay at a water depth of 37.2 m, where the influence of residual and/or tidal currents from the Akashi Strait is apparent (Yasuhara and Irizuki, 2001). *K. japonica*, *Ko. donghaiensis* and *A. nipponica* are common at water depths of more than 15–20 m in shallow sea areas around Japan (e.g., Yasuhara and Irizuki, 2001; Yamane, 1998; Bodergat and Ikeya, 1988; Frydl, 1982; Ishizaki, 1971).

The distribution of species suggests that biofacies LS is interpreted as ranging from an outer bay to the open sea at a water depth of 30–40 m, under the influence of residual and/or tidal currents from the strait.

(2) *Biofacies PT* (*Pontocythere* spp.-*Trachyleberis scabrocuneata* biofacies).—Biofacies PT is composed of two samples and lies in the lower part of core T2. It is characterized by the dominance of *Pontocythere* spp., *Trachyleberis scabrocuneata* (Brady), *S. quadriaculeata* and *Loxoconcha uranouchiensis* Ishizaki, with smaller numbers of *Loxoconcha pulchra* Ishizaki and *Nipponocythere bicarinata* (Brady). Intertidal and phytal species (*Aurila* spp. except *A. munechikai* and *A. spinifera* s.l., *Australimoosella tomokoae*, *Cornucoquimba tosaensis*, *Hemicytherura* spp., *Loxoconcha* spp. except *L. optima*, *L. pulchra*, *L. tosaensis*, *L. uranouchiensis* and *L. viva*, *Neonesidea oligodentata*, *Paradoxostomatidae* spp., *Pseudoaurila japonica*, *Robustaurila* spp., *Sclerochilus* sp., *Semicytherura* spp. and *Xestoleberis* spp.) are also common.

*Pontocythere* spp. are found in a range of habitats, from the sandy coasts of outer bays to open sea areas and/or river mouths (e.g., Ishizaki, 1968; Ikeya and Hanai, 1982; Yamane, 1998). *T. scabrocuneata* is abundant in middle to outer bay regions (Yasuhara and Irizuki, 2001). *L.*





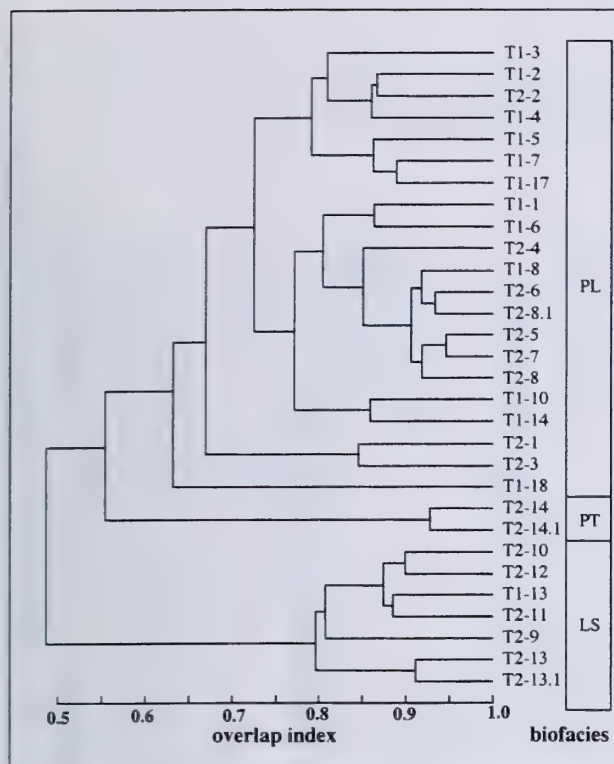


Figure 4. Dendrogram from Q-mode cluster analysis. PL, PT and LS represent the three biofacies found.

*uranouchiensis* is common in sandy bay coasts and abundant at water depths of less than 10 m (Frydl, 1982). *L. pulchra* is an estuarine inhabitant of Hiuchi-nada Bay, Seto Inland Sea, western Japan, that prefers low salinity and a water depth of less than 4 m (Yamane, 1998). *N. bicarinata* is common at water depths of more than 15 m in Osaka Bay (Yasuhara and Irizuki, 2001). However, species common at water depths of more than 15–20 m in shallow sea areas around Japan (e.g., *K. japonica*, *Ko. donghaiensis*, *A. nipponica*) are either rare or absent in this biofacies. Intertidal and phytal species could have been transported to this area by wave action or coastal currents.

Thus, biofacies PT is interpreted as ranging from a bay coast to an outer bay, near a river mouth, with water depths

of less than 15–20 m.

(3) *Biofacies PL* (*Pontocythere* spp.—*Loxoconcha optima biofacies*).—Biofacies PL is composed of 21 samples and lies in the upper part of cores T1 and T2, and also in the lower part of the T1 core. It is characterized by the dominance of *Pontocythere* spp., *Loxoconcha optima* Ishizaki, *L. pulchra* and intertidal and phytal species. *K. japonica*, *Ko. donghaiensis* and *A. nipponica* also occur in this biofacies.

*L. optima* is reported from a sandy coast, ranging from an outer bay to the open sea (Ishizaki, 1968). Those species which are common in biofacies LS, such as *C. kumaii*, *A. obai* and *F. hayamii*, are either rare or completely absent.

Biofacies PL is therefore interpreted as a sandy coast, ranging from an outer bay to the open sea, near a river mouth at water depths of more than 15–20 m, but shallower than biofacies LS.

### Temporal changes of depositional environments

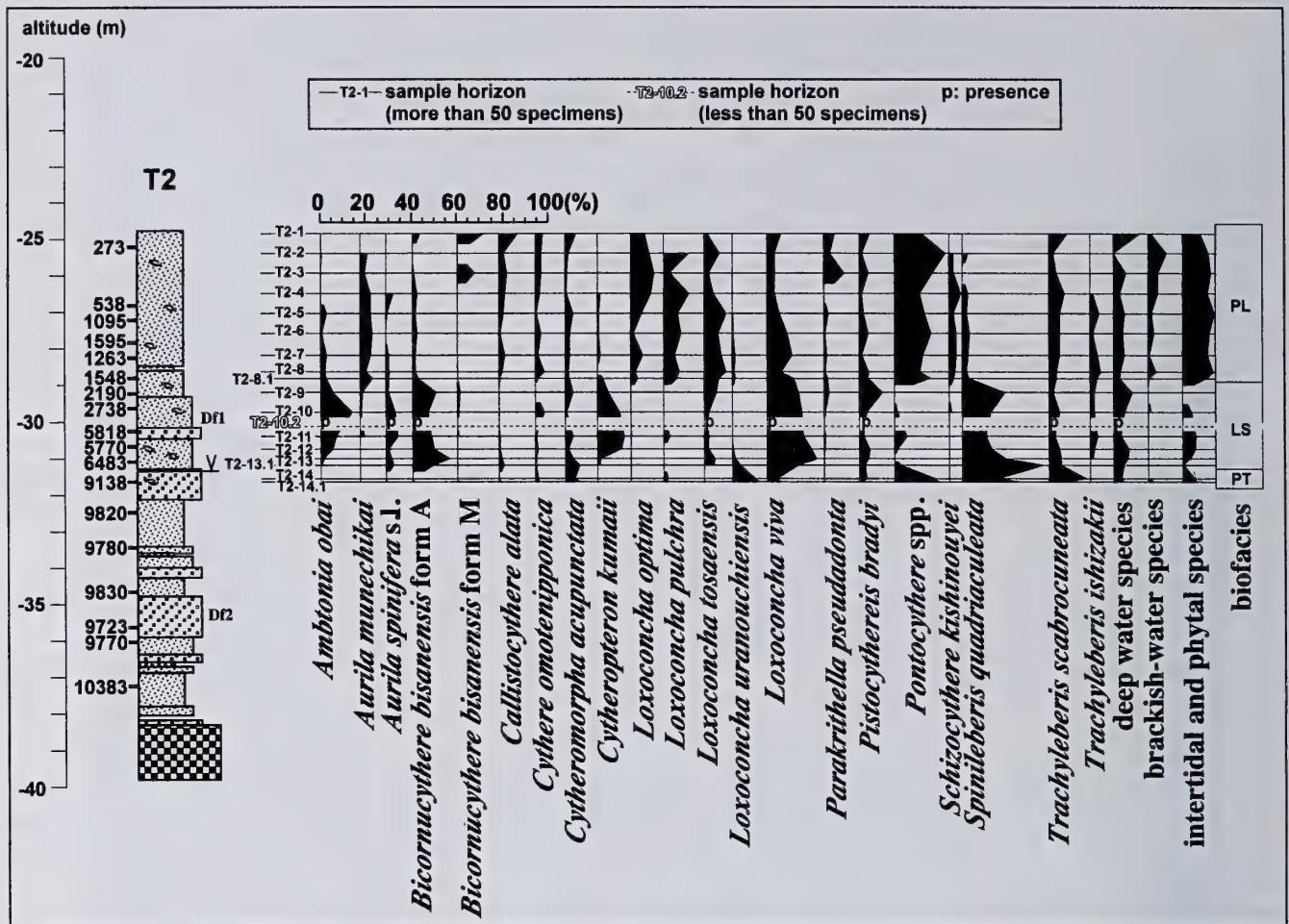
Radiocarbon dating was conducted using 31 samples from cores T1 and T2 (Nanayama *et al.*, 1999). We calibrated these radiocarbon ages using INTCAL98 (Stuiver *et al.*, 1998), because this was not done in the original study. Many of the radiocarbon ages in core T1 were reversed (Figure 6): we therefore used the radiocarbon ages from core T2 to date temporal changes in depositional environments. Correlations between cores T1 and T2 are based on Nanayama *et al.* (1999).

Based on the results of Q-mode cluster analysis, vertical changes in depositional environments and associated ostracode faunas in these cores are distinguished as follows:

*Before ca. 7,000 cal yr BP.*—This period is represented by biofacies PT, composed of two samples in core T2 (T2-14 and 14.1), and the lower part of biofacies PL, composed of three samples in core T1 (T1-14, 17 and 18).

It is considered that during this period the T2 drilling site ranged from a bay coast to an outer bay, near a river mouth, with water depth shallower than 15–20 m. At the same time, the T1 site was on the sandy coast, ranging from an

Figure 3. Scanning electron micrographs of fossil ostracodes from drilling cores in the Kitan Strait off Wakayama City. Scale bars = 1.0 mm (A for 1–19; B for 20–22). All specimens are adult left valves, except one specimen in Fig. 4.21 (an adult right valve). 1. *Callistocythere hayamensis* Hanai (sample no. T1-8). 2. *Callistocythere alata* Hanai (sample no. T1-6). 3. *Callistocythere asiatica* Zhao (sample no. T2-3). 4. *Callistocythere undata* Hanai (sample no. T2-4). 5. *Callistocythere* sp. 1 (sample no. T2-8). 6. *Ishizakiella miurensis* (Hanai) (sample no. T2-3). 7. *Loxoconcha pulchra* Ishizaki (sample no. T1-8). 8. *Loxoconcha optima* Ishizaki (sample no. T1-8). 9. *Loxoconcha tosaensis* Ishizaki (sample no. T1-6). 10. *Loxoconcha viva* Ishizaki (sample no. T2-8.1). 11. *Parakrithella pseudadonta* (Hanai) (sample no. T1-6). 12. *Cytheromorpha acupunctata* (Brady) (sample no. T1-6). 13. *Spinileberis quadriaculeata* (Brady) (sample no. T2-13.1). 14. *Falsobuntonia hayamii* (Tabuki) (sample no. T2-9). 15. *Xestoleberis opalescenta* Schornikov (sample no. T2-3). 16. *Perissocytheridea* sp. (sample no. T2-2). 17. *Phlyctocythere japonica* Ishizaki (sample no. T2-14). 18. *Neopellucistoma inflatum* Ikeya and Hanai (sample no. T2-2). 19. *Ambtonia obai* (Ishizaki) (sample no. T2-12). 20. *Aurila spinifera* s.l. Schornikov and Tsareva (sample no. T2-13). 21. *Cletocythereis* sp. (sample no. T2-6). 22. *Trachyleberis scabrocuneata* (Brady) (sample no. T1-7).



**Figure 5.** Columnar section of core T2, sample horizons, radiocarbon ages (cal yr B.P.), biofacies and percentages of dominant ostracode species. Deep-water species are *Amphileberis nipponica*, *Falsobuntonia hayamii*, *Kobayashiina donghaiensis*, *Krithe japonica* and *Nipponocythere bicarinata*. Brackish water species are *Cytherura mii*, *Darwinula* sp., *Ishizakiella miurensis*, *Perissocytheridea japonica*, *Perissocytheridea* sp., *Spinileberis furuyaensis* and *Spinileberis pulchra*. Intertidal and phytal species are *Aurila* spp. except *A. munechikai* and *A. spinifera* s.l., *Australimoesella tomokoae*, *Cornucoquimba tosaensis*, *Hemicytherura* spp., *Loxoconcha* spp. except *L. optima*, *L. pulchra*, *L. tosaensis*, *L. uranouchiensis* and *L. viva*, *Neonesidea oligodentata*, *Paradoxostomatidae* spp., *Pseudoaurila japonica*, *Robustaurila* spp., *Sclerochilus* sp., *Semicytherura* spp. and *Xestoleberis* spp.

outer bay to the open sea, near a river mouth, with water depths of more than 15–20 m. Species that are common at water depths of more than 15–20 m in shallow sea areas around Japan (e.g., *A. obai*, *K. japonica*, *Ko. donghaiensis* and *A. nipponica*) are, however, absent in samples T1-17 and T1-18. In these horizons, it is considered that water depths were shallower than the other horizons.

**Ca. 7,000–2,000 cal yr BP.**—This period is represented by biofacies LS, and is composed of six samples in core T2 (T2-9, 10, 11, 12, 13 and 13.1), and one sample in core T1 (T1-13).

These sites ranged from an outer bay to the open sea at water depths of 30–40 m, and were influenced by residual and/or tidal currents from the strait.

**After ca. 2,000 cal yr BP.**—This period is represented by biofacies PL and is composed of nine samples in core T2 (T2-1, 2, 3, 4, 5, 6, 7, 8 and 8.1), and also the upper part of biofacies PL, which is composed of nine samples in core T1 (T1-1, 2, 3, 4, 5, 6, 7, 8 and 10).

These sites were at the sandy coast, ranging from an outer bay to the open sea, near a river mouth, with water depths greater than 15–20 m, but shallower than biofacies LS. The percentage of those species that are common at water depths of more than 15–20 m in shallow sea areas around Japan (e.g., *A. obai*, *K. japonica*, *Ko. donghaiensis* and *A. nipponica*) are smaller in core T1 than in core T2. This indicates that the T1 site was in shallower water than the T2 site during this period.



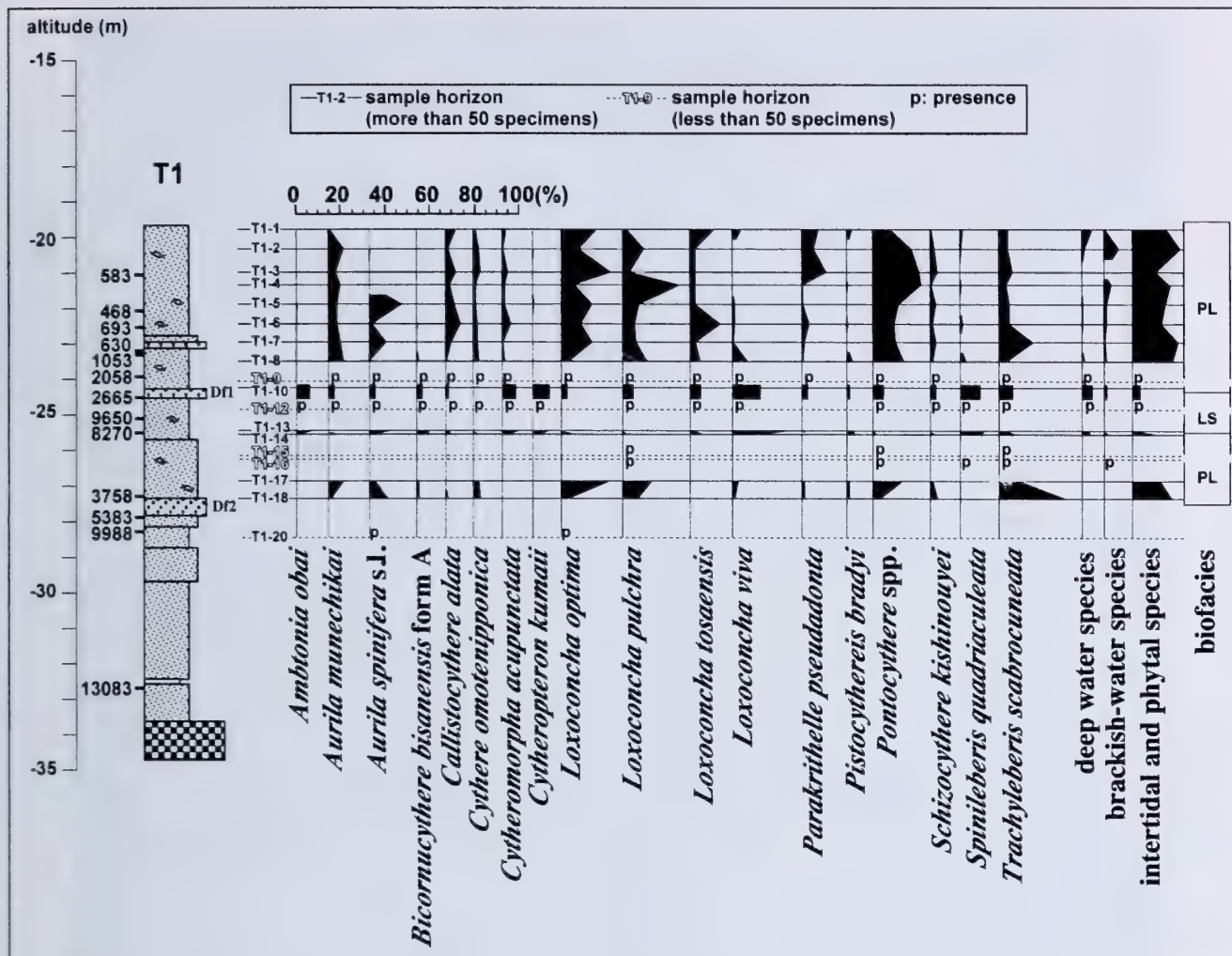


Figure 6. Columnar section of core T1, sample horizons, radiocarbon ages (cal yr B.P.), biofacies and percentages of dominant ostracode species. Deep-water, brackish, and intertidal and phytal species are similar to those in Figure 5.

In the Osaka Plain and the inner part of Osaka Bay, the relative sea-level change has been studied in detail on the basis of sedimentary facies, fossil ostracode faunas and high-density radiocarbon dating of molluscan shells (Miyahara *et al.*, 1999; Masuda *et al.*, 2000; Masuda and Miyahara, 2000; Irizuki *et al.*, 2001). These studies reported that the sea level rose rapidly from the period between ca. 11,000 cal yr BP to ca. 5,300–5,000 cal yr BP and from that time fell to the present sea level. The maximum sea level highstand was at ca. 5,300–5,000 cal yr BP in Osaka Bay (Masuda *et al.*, 2000). The historical changes in water depth at the two sites investigated in this study are similar to the relative sea-level changes proposed by Masuda *et al.* (2000), although the cores reveal areal differences in faunal changes during the same period. This result suggests that the relative sea-level curve of Masuda

*et al.* (2000) lends itself to the standard for relative sea-level change not only in Osaka Bay but also in more wide areas.

### Systematic descriptions

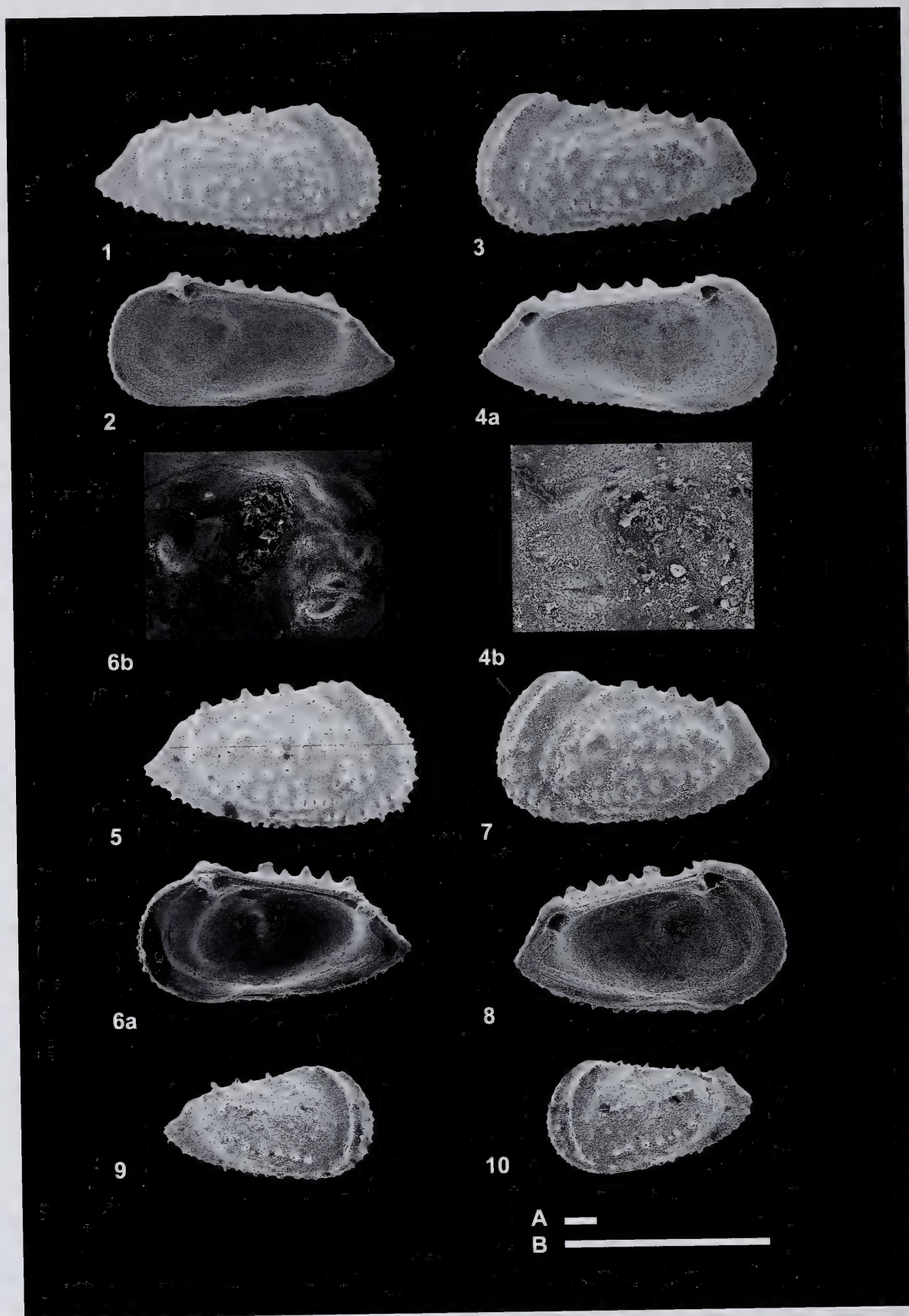
All the illustrated specimens are deposited in the collections of the Department of Biology and Geosciences, Graduate School of Science, Osaka City University (OCUCO).

Suborder Podocopina Sars, 1866

Superfamily Darwinuloidea Brady and Norman, 1889

Family Darwinulidae Brady and Norman, 1889

Genus *Darwinula* Brady and Robertson in Jones, 1885





*Darwinula* sp.

Figure 8.5–8.8

*Materials*.—20 specimens.*Diagnosis*.—*Darwinula* characterized by elongate and small carapace.*Occurrence*.—T1–2, 4–6, 8, T2–2 to T2–4, 6, 8, 10.*Remarks*.—This species has central muscle scars characteristic of darwinulids. This is the first fossil record of the genus from the Japanese Holocene. Ikeya and Hanai (1982) attributed a single broken valve from the Recent of Hamana-ko Bay, central Japan, to this genus. This genus has a freshwater habitat (Van Morkhoven, 1963).

Superfamily Cytheroidea Baird, 1850

Family Trachyleberididae Sylvester-Bradley, 1948

Subfamily Trachyleberidinae Sylvester-Bradley, 1948

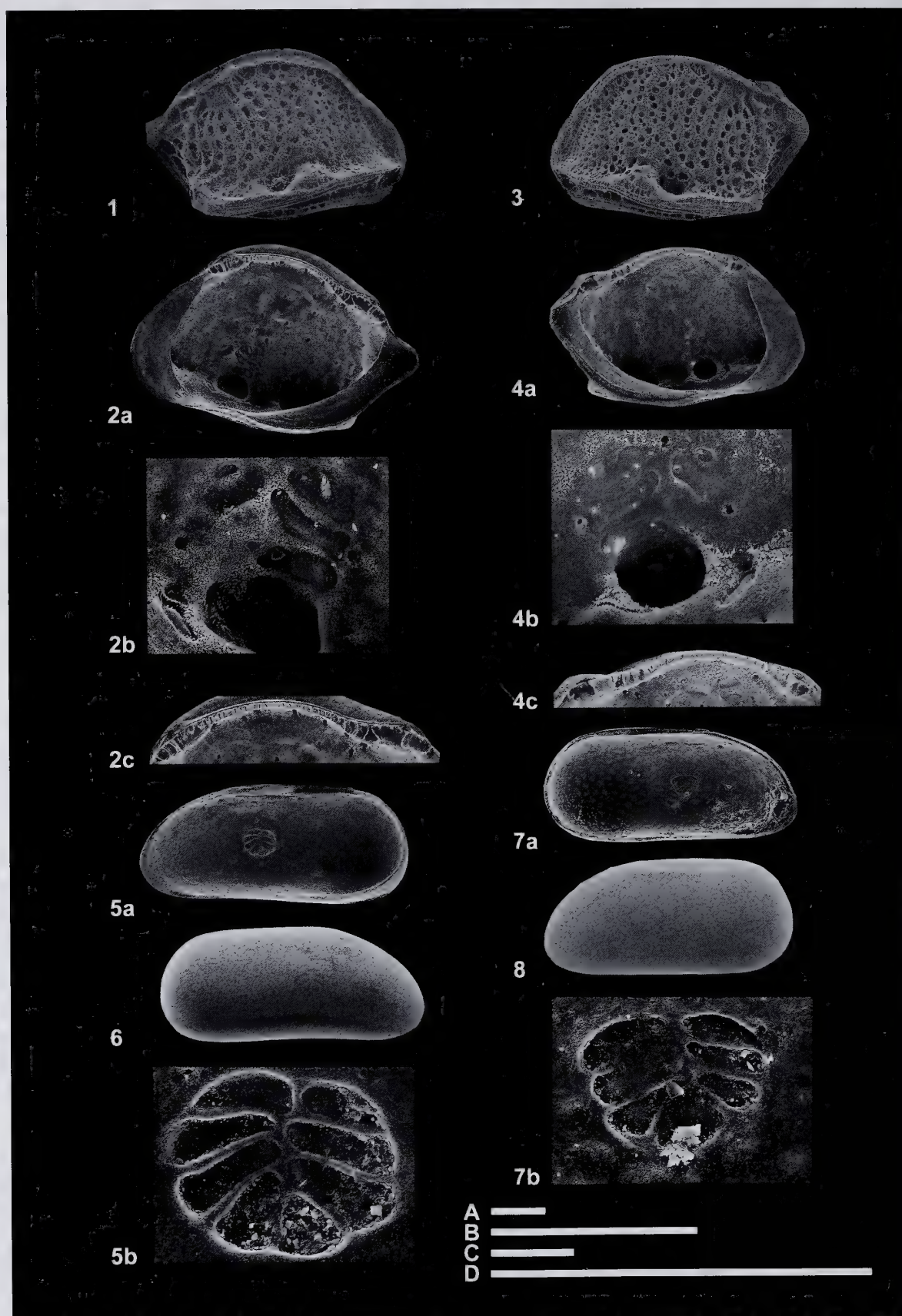
Tribe Trachyleberidini Sylvester-Bradley, 1948

Genus *Trachyleberis* Brady, 1898*Trachyleberis ishizakii* sp. nov.

Figure 7.1–7.10

*Cythereis Yamigera* [sic] (Brady). Kajiyama, 1913, p. 12, pl. 1, 64–66.*Trachyleberis scabrocuneata* (Brady). Ishizaki, 1969, p. 221–222, pl. 26, fig. 8; Ishizaki, 1971, p. 92–93, pl. 4, fig. 16; Okubo, 1979, p. 156, fig. 7a, b; Ikeya and Compton, 1983, p. 120, pl. 10–120, figs. 1a–4b, p. 126, pl. 10–126, figs. 1a–4b; Paik and Lee, 1988, p. 550, pl. 2, fig. 11; Ikeya and Itoh, 1991, p. 145, fig. 24, C; Kamiya and Nakagawa, 1993, p. 129, pl. 4, fig. 7; Ishizaki *et al.*, 1993, p. 329, fig. 7c; Irizuki *et al.*, 1998a, p. 7, fig. 2.13; Kamiya *et al.*, 2001, p. 103, fig. 18.18.*Cythere scabrocuneata* Brady. Puri and Hulings, 1976, p. 289, pl. 26, figs. 6, 8.*Trachyleberis* sp. 1. Ikeya and Suzuki, 1992, p. 137, pl. 9, fig. 4.*Actinocythereis* sp. Kamiya and Nakagawa, 1993, p. 129, pl. 4, fig. 8.*Trachyleberis* sp. Irizuki *et al.*, 2001, p. 109, fig. 3.8; Yasuhara and Irizuki, 2001, p. 95, pl. 12, figs. 9–13.*Etymology*.—In honor of Dr. Kunihiro Ishizaki.*Materials*.—86 specimens.*Diagnosis*.—*Trachyleberis* characterized by subtriangular valve shape, tubercles on valve surface, large dorsal tubercles and anterior marginal ridge.*Description*.—Carapace large, subtriangular, tapering posteriorly in lateral view, highest at anterior cardinal angle. Anterior margin broadly rounded and slightly extended below. Dorsal margin straight. Ventral margin broadly convex in female and straight in male. Posterior margin acuminate. Anterior, ventral and posterior margins fringed by spines and tubercles. Surface ornamented with tubercles, subcentral tubercle and anterior marginal ridge. Anterior marginal ridge running from anterior cardinal angle to midpoint of anterior margin. Eye and subcentral tubercles distinct. Pore canal openings moderate in number, scattered on most of valve surface. Pore canals with opening along edge of marginal contact zone of ventral marginal surface straight, numerous along anterior and posteroventral margins. Marginal infold moderate in width along anterior and posterior margins. No vestibule. Hinge holamphidont. Muscle scars consisting of one V-shaped frontal scar and a row of four adductor scars. Sexual dimorphism distinct; males more slender than females.*Types*.—Holotype, sample no. T1–6, OCUCO 0005, male RV, L = 0.884 mm, H = 0.420 mm (Figure 7.1); 9 paratypes, sample nos. T2–8.1, OCUCO 0006, T2–7, OCUCO 0007, T2–8, OCUCO 0008, T2–7, OCUCO 0009, T2–8.1, OCUCO 0010, T2–8.1, OCUCO 0011, T2–8, OCUCO 0012, T1–6, OCUCO 0013 and T1–6, OCUCO 0014.*Type locality*.—Holocene sediments off Wakayama City (34° 14.7' N, E 135° 5.2' E).*Occurrence*.—T1–2, 5–10, 13, 14, 18, T2–4 to T2–8, 8.1, 9, 10, 11–13.*Remarks*.—This species is similar to *Trachyleberis scabrocuneata* (Brady, 1880), but differs in having a shorter anterior marginal ridge, smaller carapace, straight margin broadly convex in male, larger dorsal tubercles, smaller number of surface tubercles and more slender shape. Also, this species is similar to *Trachyleberis niitsumai* Ishizaki, 1971, but differs in having a shorter anterior marginal ridge, more prominent and regular surface tubercles, larger dorsal tubercles and more slender shape.

◀ **Figure 7.** *Trachyleberis ishizakii* sp. nov. 1. Lateral view of male RV, holotype, T1–6, OCUCO 0005, L = 0.884 mm, H = 0.420 mm. 2. Internal view of male RV, T2–8.1, OCUCO 0006, L = 0.883 mm, H = 0.419 mm. 3. Lateral view of male LV, T2–7, OCUCO 0007, L = 0.869 mm, H = 0.447 mm. 4a, b. Internal view and muscle scars of male LV, T2–8, OCUCO 0008, L = 0.921 mm, H = 0.439 mm. 5. Lateral view of female RV, T2–7, OCUCO 0009, L = 0.848 mm, H = 0.463 mm. 6a, b. Internal view and muscle scars of female RV, T2–8.1, OCUCO 0010, L = 0.848 mm, H = 0.445 mm. 7. Lateral view of female LV, T2–8.1, OCUCO 0011, L = 0.848 mm, H = 0.476 mm. 8. Internal view of female LV, T2–8, OCUCO 0012, L = 0.852 mm, H = 0.480 mm. 9. Lateral view of A–1 stage RV, T1–6, OCUCO 0013, L = 0.656 mm, H = 0.359 mm. 10. Lateral view of A–1 stage LV, T1–6, OCUCO 0014, L = 0.641 mm, H = 0.362 mm. Scale bars are 0.1 mm: A for 1–4a, 5–6a and 7–10; B for 6b and 4b.





Family Cytheruridae G.W. Müller, 1894  
 Subfamily Cytheropterinae Hanai, 1957  
 Genus *Cytheropteron* Sars, 1866

*Cytheropteron kumaii* sp. nov.

Figure 8.1–8.4

*Cytheropteron miurense* Hanai. Ikeya and Itoh, 1991, p. 136, fig. 15, A.

*Cytheropteron* sp. Yasuhara and Irizuki, 2001, p. 79, pl. 4, fig. 10.

**Etymology.**—In honor of Prof. Hisao Kumai.

**Materials.**—80 specimens.

**Diagnosis.**—*Cytheropteron* characterized by subrhomboidal valve shape, small carapace and straight ventral alar process.

**Description.**—Carapace small, subrhomboidal in lateral view, highest at midlength. Anterior margin obliquely rounded. Dorsal margin strongly arched. Ventral margin sinuate, concave in middle, obscured in posterior third by alar process. Posterior margin protruding into a horizontally pointed caudal process. Surface ornamented with numerous reticula aligned more or less vertically, and dorsal and ventral marginal ridges. Reticula coarser in posterior half. Dorsal marginal ridge arcuate, very narrow, running along dorsal margin from anterior third to posterior terminal. Ventral marginal ridge starting from anterior end and running along ventral margin to form a prominent anterior edge of alar process. Eye tubercle indistinct. Pore canal openings moderate in number, scattered on most of valve surface. Pore canals with openings along edge of marginal contact zone of ventral marginal surface few, approximately ten along anterior margin. Marginal infold moderate in width along anterior and posterior margins. Vestibule poorly developed along anterior margin, broadest at anteroventral margin. Hinge line sinuous in interior view. Hinge of right valve consists of anterior and posterior teeth and an intermediate groove. Intermediate groove subdivided into three parts: short anterior part with three large crenulations, finely crenulate median part and concave posterior part with six small sockets, of which the anterior three are clearly separated and the posterior three are connected to each other. Hinge of left valve complementary of that of right valve. Muscle scars consist of two frontal scars, of which upper scar is smaller and lower scar is elongate, and a row of four elongate adductor scars.

Sexual dimorphism indistinct.

**Type and Dimensions.**—Holotype, sample no. T2-12, OCUCO 0015, adult LV, L = 0.482 mm, H = 0.313 mm (Figure 8.3); 3 paratypes, sample nos. T1-12, OCUCO 0016, T1-12, OCUCO 0017 and T2-12, OCUCO 0018.

**Type locality.**—Holocene sediments off Wakayama City (34° 14.5' N, 135° 5.2' E).

**Occurrence.**—T1-2, 5, 10, 12-14, T2-4 to T2-7, 8.1, 9, 10, 11-13, 13.1.

**Remarks.**—This species is similar to *Cytheropteron miurense*, but differs in having a thinner alar process and finer and larger amount of surface ornamentation.

### Conclusions

1. Before ca. 7,000 cal yr BP, site T2 ranged from a bay coast to an outer bay, near a river mouth, at water depths of less than 15–20 m, and site T1 was a sandy coast, ranging from an outer bay to the open sea, near a river mouth, at water depths of more than 15–20 m, but shallower than biofacies LS.

2. From ca. 7,000–2,000 cal yr BP, the two sites varied in condition from an outer bay to the open sea at water depths of 30–40 m, where they were strongly influenced by the residual and/or tidal currents from the strait.

3. After ca. 2,000 cal yr BP, the two sites were situated along a sandy coast, ranging from an outer bay to the open sea, near a river mouth, at water depths of more than 15–20 m, but shallower than biofacies LS. Site T1 was shallower than site T2 during this period.

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← **Figure 8.** 1–4, *Cytheropteron kumaii* sp. nov. 1. Lateral view of adult RV, T1-12, OCUCO 0016, L = 0.482 mm, H = 0.326 mm. 2a–c. Internal view, muscle scar and hinge of adult RV, T1-12, OCUCO 0017, L = 0.530 mm, H = 0.349 mm. 3. Lateral view of adult LV, holotype, T2-12, OCUCO 0015, L = 0.482 mm, H = 0.313 mm. 4a–c. Internal view, muscle scars and hinge of adult LV, T2-8, OCUCO 0018, L = 0.474 mm, H = 0.299 mm. 5–8, *Darwinula* sp. 5a–b. Internal view and muscle scars of adult RV, T2-8, OCUCO 0001, L = 0.494 mm, H = 0.226 mm. 6. Lateral view of adult RV, T2-4, OCUCO 0002, L = 0.487 mm, H = 0.227 mm. 7a–b. Internal view and muscle scars of adult LV, T1-2, OCUCO 0003, L = 0.469 mm, H = 0.222 mm. 8. Lateral view of adult LV, T2-4, OCUCO 0004, L = 0.462 mm, H = 0.226 mm. Scale bars are 0.1 mm: A for 1–2a, 3–4a, 5a, 6, 7a and 8; B for 2b and 4b; C for 2c and 4c; D for 5b and 7b.

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# Taphonomy of the bivalve assemblages in the upper part of the Paleogene Ashiya Group, southwestern Japan

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**Abstract.** The Paleogene Ashiya Group, in which molluscan fossils are abundant (= Ashiya fauna), consists mainly of shallow marine deposits that exhibit sedimentary cycles especially in the Waita Formation (upper part of the Group). Each cycle is redefined as a thin transgressive basal sandstone (transgressive systems tract) overlain by a progradational coarsening-upward interval (highstand systems tract). The depositional environment varies from a shallower condition influenced by strong wave action (shoreface?) to a deeper condition below the storm wave base, which is followed by next shallower conditions such as lower shoreface or intertidal zone. Molluscan fossils occur only from the thin lower part of each cycle, namely the transgressive basal sandstone and from the mudstone of the earliest progradational phase. The fossils occur both as shell concentrations and more dispersed fossiliferous deposits. Bed-by-bed sampling based on taphonomic, sedimentologic and paleoecologic observations distinguishes four fossil assemblages, (a) *Glycymeris-Phacosoma*, (b) *Venericardia-Crassatella*, (c) *Venericardia* and (d) *Yoldia-Nucula*. These assemblages occur successively in each cycle, and their taphonomic features also change upward from a wave-generated allochthonous shellbed on the basal ravinement surface to autochthonous shell patches. The successive change accompanies a decreasing wave-influence during a transgressive period. Epibionts, such as epifaunal byssally attached bivalves and barnacles, occur abundantly as associated species of the *Venericardia-Crassatella* assemblage from the middle part of the transgressive basal sandstone. Epibiontic colonization probably reflects taphonomic feedback, with shelly substrates avoiding burial by the winnowing of sediments during transgression. Autochthonous shellbeds dominated by *Venericardia subnipponica* are intercalated in the glauconitic sandstone beds (surface of maximum transgression) at the top of the transgressive basal sandstone. The shellbeds probably represent an attritional accumulation with dead shells of *Venericardia* supplied continuously *in situ* during a phase of low sediment supply.

**Key words:** Ashiya Group, bivalves, paleoecology, Paleogene, sedimentary cycle, transgression

## Introduction

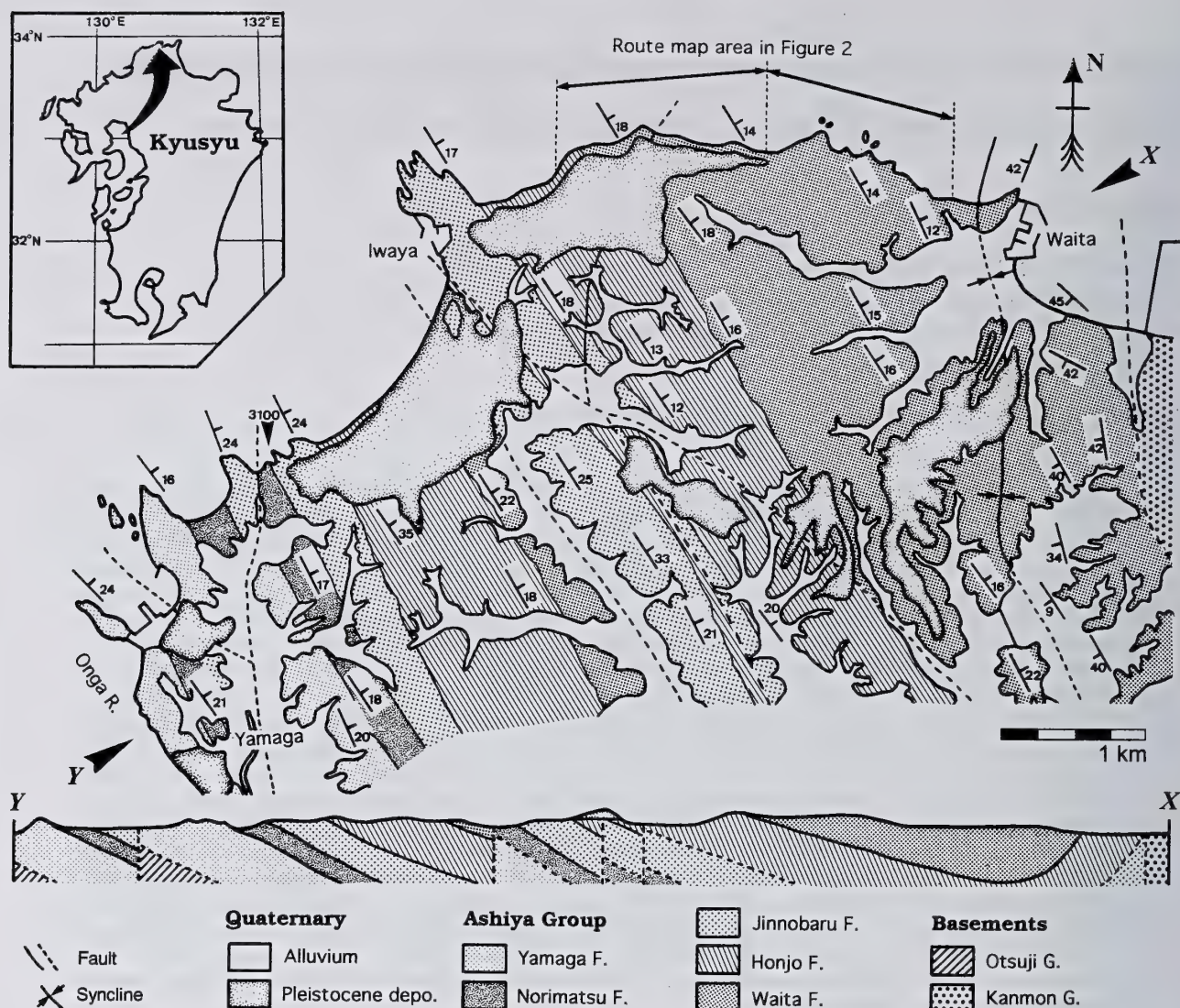
The Ashiya Group is the uppermost sequence of coal-bearing Paleogene deposits in the northern limb of Kyushu. It consists of shallow marine sandstones and mudstones, and is biostratigraphically assigned to the latest Early Oligocene age by calcareous nannoplankton and foraminifera (Saito and Okada, 1984; Tsuchi *et al.*, 1987). It was lithostratigraphically subdivided into the Yamaga, Sakamizu, and Waita Formations in upward sequence (Nagao, 1927a, 1928a; Okabe and Ohara, 1972 *etc.*). Recently the stratigraphic division was revised by Ozaki *et al.* (1993), in which the Yamaga, Norimatsu, Jinnobaru, Honjo and Waita Formations were redefined. Hayasaka (1991) investigated the group sedimentologically, distinguished 23

coarsening-upward sedimentary cycles, and gave their environmental interpretations.

Abundant molluscan fossils from the Group are called the Ashiya Fauna and represent the typical molluscan fauna of Oligocene age in west Japan (Nagao, 1927a, 1928a; Otsuka, 1939; Oyama *et al.*, 1960 *etc.*). The molluscan fossils have been taxonomically and biostratigraphically studied by several authors (Nagao, 1927b, 1928b; Mizuno, 1963 *etc.*). In addition, the molluscan fauna from the Jinnobaru Formation was studied paleoecologically (Shuto and Shiraishi, 1971).

However, little is known about the precise relation between sedimentary cycles and the molluscan assemblages, which exhibit characteristic modes of occurrence by facies. Taphonomic features of the molluscan assemblages also re-





**Figure 1.** Geologic map of the Wakamatsu area, Kitakyushu, northern Kyushu. Route-mapped area in Figure 2 indicated by thick arrows and Locality 3100 are shown.

main largely to be investigated.

To clarify these problems, I closely examined the sedimentary features and modes of fossil occurrence of the Ashiya Group bed-by-bed. Through detailed observations, particularly in the Waita Formation (the upper part of the Group), I discovered a close relationship between the sedimentary cycle and the composition and mode of occurrence of bivalve assemblages. These changes are commonly repeated in every cycle of the Waita Formation.

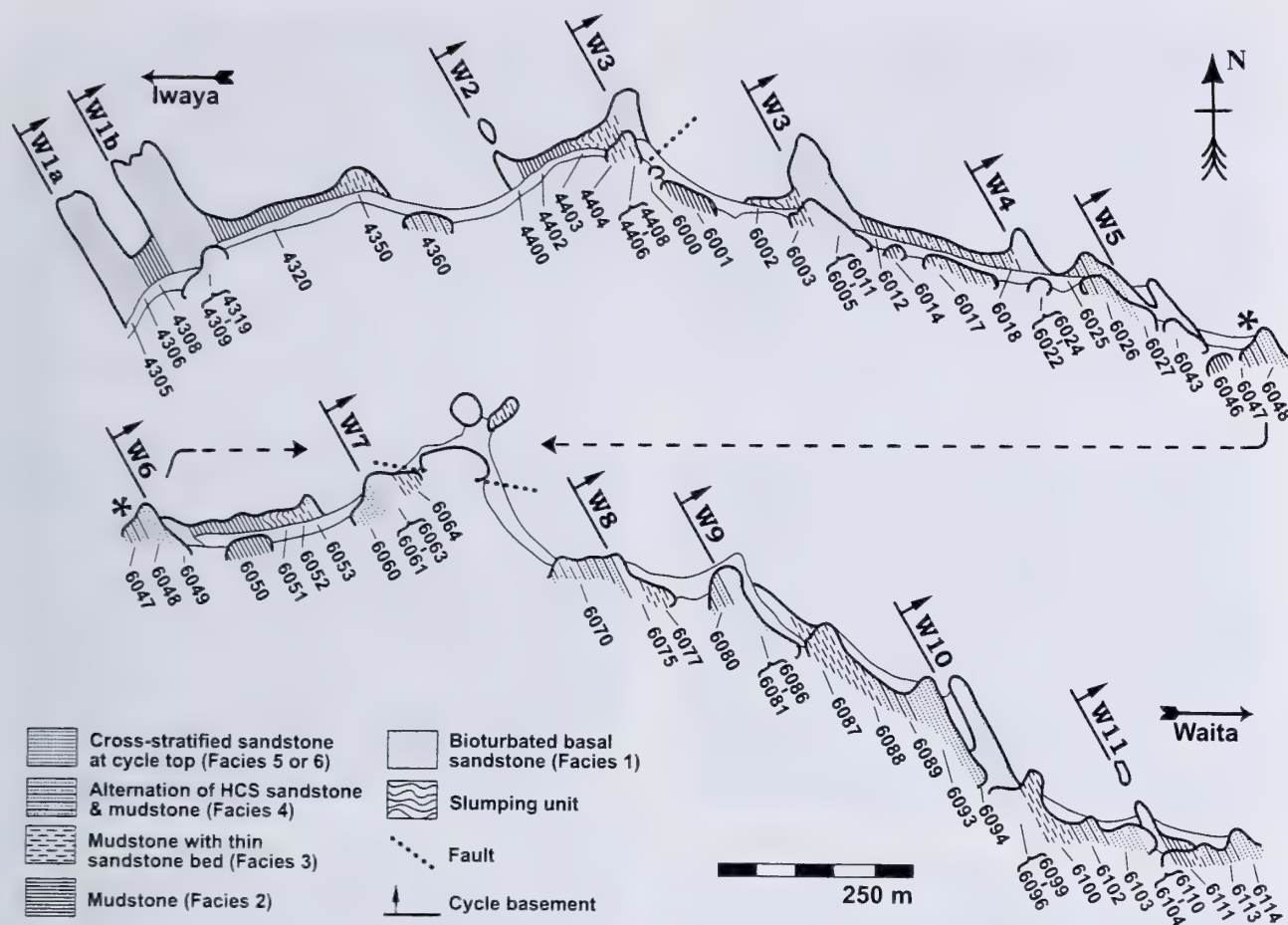
This paper aims to reconstruct the sedimentological and paleoecological processes in the Ashiya Group based on detailed observations of its sedimentological and taphonomic features. My aims here are to: (1) redefine the sedimentary cycles in the Waita Formation and describe its

lithofacies, (2) describe modes of occurrence and the succession of the molluscan assemblages in the cycle, and (3) discuss the formative process of the sedimentary and paleoecological succession.

### Geological setting

The Ashiya Group in the study area is bounded on the east by a fault of NNW-SSE trend, and on the west by the Onga River. The strata of the group strike N 20–45° W and dip 10–30° gently northeastward except for those in the eastern limb of the syncline (Figure 1). In the eastern limb, the strata steeply strike N 10–50° W and dip 45° W. At least seven faults of similar NW-SE trend are observed





**Figure 2.** Route map from the Iwaya to Waita coast (Figure 1). The left section connected to the right at the asterisks (\*). Localities and redefined sedimentary cycles are shown.

or estimated.

The Ashiya Group is subdivided into the Yamaga, Norimatsu, Jinnobaru, Honjo and Waita Formations in ascending order (Ozaki *et al.*, 1993). The lowermost Yamaga Formation is characterized by bioturbated fine sandstones. The formation is more than 170 m thick, although the basal part is unexposed. The succeeding Norimatsu Formation consists of the alternating sandstone and mudstone, and is 50–70 m thick. Both formations crop out in the western part of the study area (Figure 1).

The Jinnobaru Formation consists of sandstones in which hummocky cross-stratification is occasionally observed, and is 140–260 m thick. The Honjo Formation consists of sandstones and mudstones, exhibits sedimentary cycles, and is about 230 m thick. Both formations crop out in the central part of the area from north to south (Figure 1).

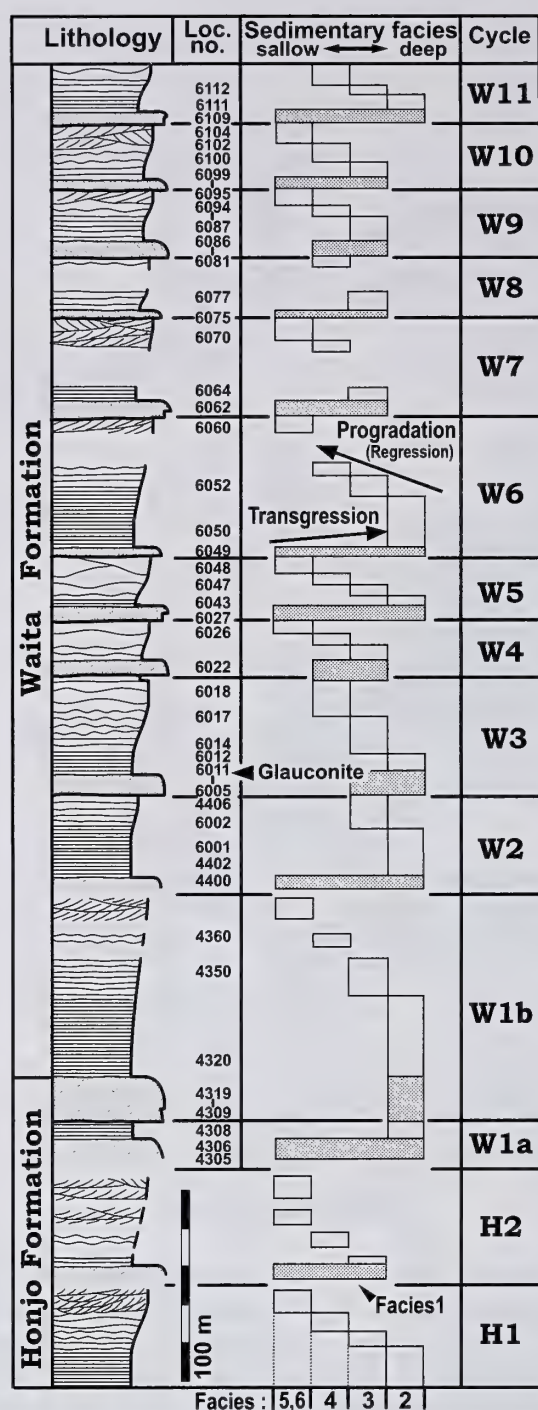
The Waita Formation (uppermost of the Group) exhibits clear sedimentary cycles composed of sandstones and mudstones (Figure 2). It is widely distributed in the east-

ern part of the area, and is more than 450 m thick, although the top part is unexposed (Figure 1).

### Sedimentary cycles

The upper part of the Ashiya Group (Honjo and Waita Formations) consists of coarsening-upward sedimentary cycles (Hayasaka, 1991; Ozaki *et al.*, 1993). Each cycle is 30–100 m thick (Figure 3), and consists of various sandstones and mudstones. At least 11 sedimentary cycles, named W1–W11 in ascending order, are recognized in the Waita Formation (Hayasaka, 1991; Ozaki *et al.*, 1993). Previous studies defined the sedimentary cycles as coarsening-upward lithologic change, which begins with a mudstone interval and ends with a sandstone interval (Hayasaka, 1991, p. 617, fig. 5; Figure 3).

However, close examination indicates that the definition of the cycles must be revised. Specifically, there is a sharp erosional surface within the upper sandstone interval of



each previous "cycle" (Figure 4A). This surface marks a distinct depositional boundary between the stratified sandstone and the mottled sandstone (Figure 3), whereas the transition from the burrowed sandstone to the overlying mudstone is continuous and gradational, as well as from the mudstone to the stratified sandstone. Therefore, it is much better to define the erosional surface as the base of each cycle. I use the names of W1-W11 to denote cycles defined in this way.

Following this revision, each cycle consists of a transgressive basal sandstone (Facies 1), which fines usually from medium sandstone upward to very fine sandstone, and the overlying progradational coarsening-upward interval (Facies 2-6; Figures 4B and 5). The latter is lithologically subdivided into five sedimentary facies: mudstone (Facies 2), mudstone interbedded with very thin sandstone beds (Facies 3), alternated HCS (hummocky cross-stratification) sandstone and mudstone (Facies 4), amalgamated HCS sandstone (Facies 5), and tabular cross-stratified sandstone (Facies 6; Figure 5). As examples, successions of the cycle W3 and W10 are shown in Figure 5.

#### Transgressive basal sandstone (Facies 1)

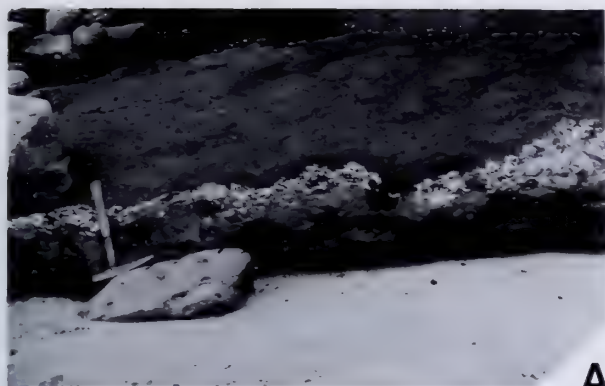
The transgressive basal sandstone (Facies 1) rests on a distinctive erosional surface truncating the upper part of the underlying cycle (Figures 3, 5), and fine upward from medium sandstone to very fine sandstone (Figure 5). This basal sandstone facies is conformably capped with mudstone of the Facies (2) or (3) (Figures 3, 5). The thickness of the basal sandstone attains 5-20 m, and is thin compared with the overlying coarsening-upward interval in each sedimentary cycle (30-100 m).

The basal sandstone is gray to greenish gray in color and includes lithic granules, grains of green smectite, and pum-

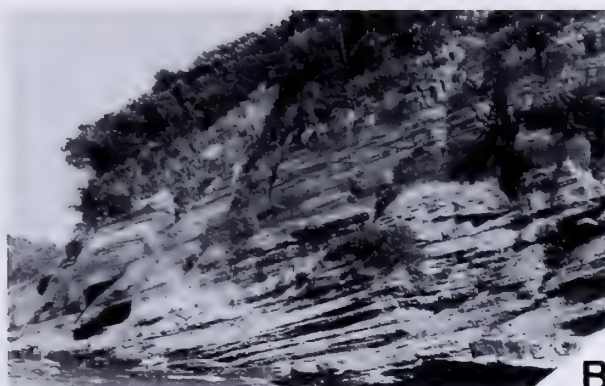
**Figure 3.** Columnar section of the Waita Formation exposed along the Iwaya to Waita coast. At least 11 sedimentary cycles, W1-W11 in ascending order, are recognized in the Waita Formation. Facies 1-6 indicate sedimentary facies in a cycle: transgressive basal sandstone (Facies 1), mudstone (Facies 2), mudstone interbedded with very thin sandstone beds (Facies 3), alternation of HCS sandstone and mudstone (Facies 4), amalgamated HCS sandstone (Facies 5), and tabular cross-stratified sandstone (Facies 6) in order. Glaucinite sandstone bed is intercalated at the top of the transgressive basal sandstone of the Cycle 3. Facies 2-4 compose the progradational coarsening-upward interval.

→ **Figure 4.** Lithofacies of the cycles in the Waita Formation. **A.** Erosional basement of the sedimentary Cycle W3, Loc. 6005. A shellbed showing a wave dune covers the erosional surface. Hammer is 30 cm long. **B.** Up-coarsening interval (Facies 2-5) in Sedimentary Cycle W5, Loc. 6047. The cliff is 15 m in height. **C.** Vertical profile of the basal sandstone (Facies 1) bioturbated by *Thalassinoides* ichnosp., Loc. 6006. (Natural size.) **D.** Vertical profile of the basal sandstone. Light-colored grains are pumice, dark-colored grains green smectite. Loc. 6098a. (Natural size) **E.** Photomicrograph of top part of basal sandstone (Facies 1), Loc. 6011a. Glaucinite grains, gray in the photograph, are abundant. Scale is 0.5 mm long. **F.** *Phycosiphon* ichnosp. in vertical profile of the mudstone with thin sheet sandstone (Facies 3), Loc. 6017. (Natural size.) **G.** *Planolites* ichnosp. in vertical profile of alternation of HCS sandstone and mudstone (Facies 4), Loc. 6102. (Natural size) **H.** Amalgamated HCS sandstone (Facies 5), Loc. 6026. Hammer is 30 cm long.

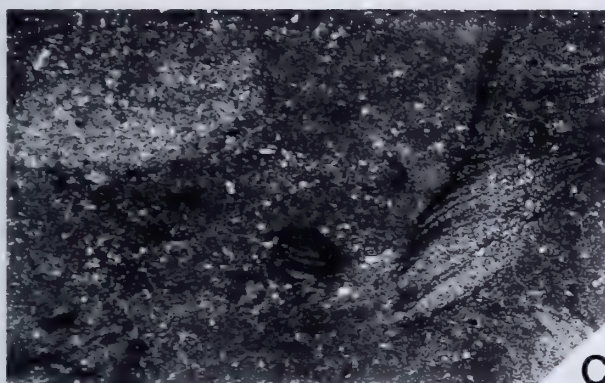




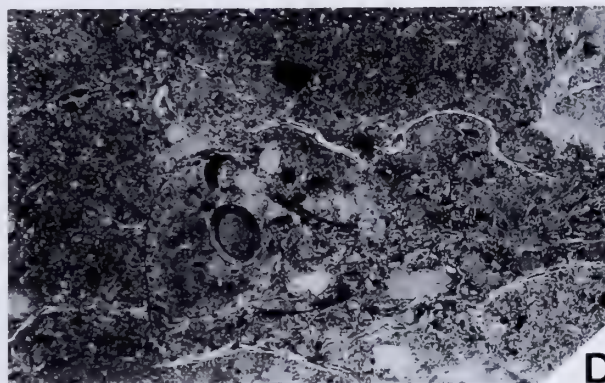
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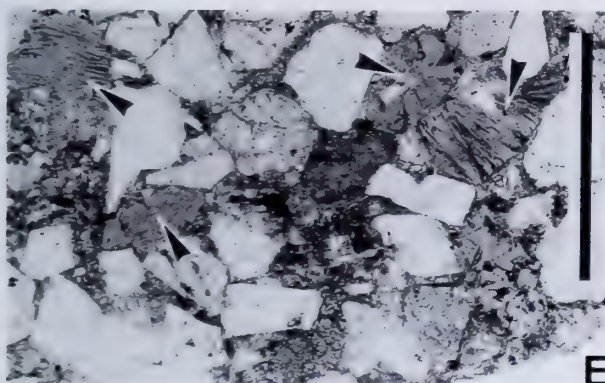
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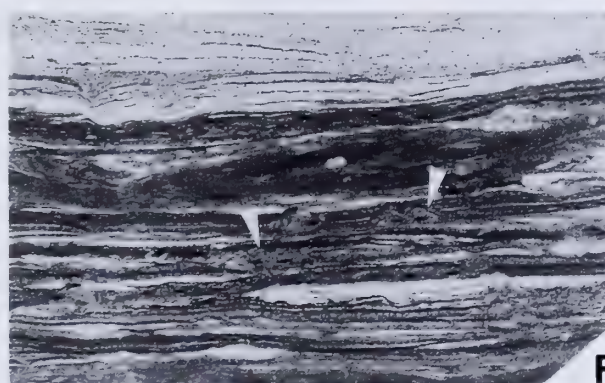
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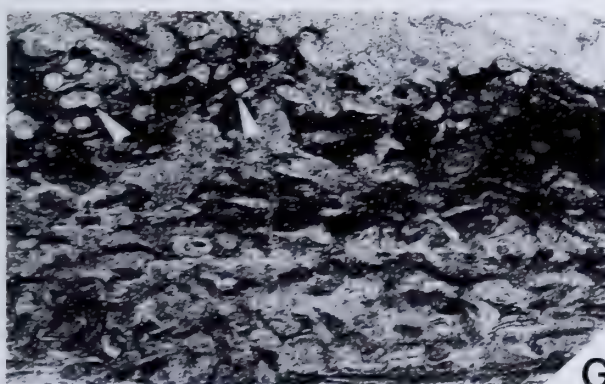
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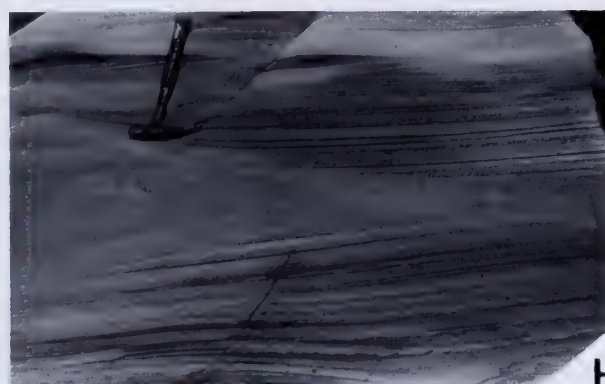
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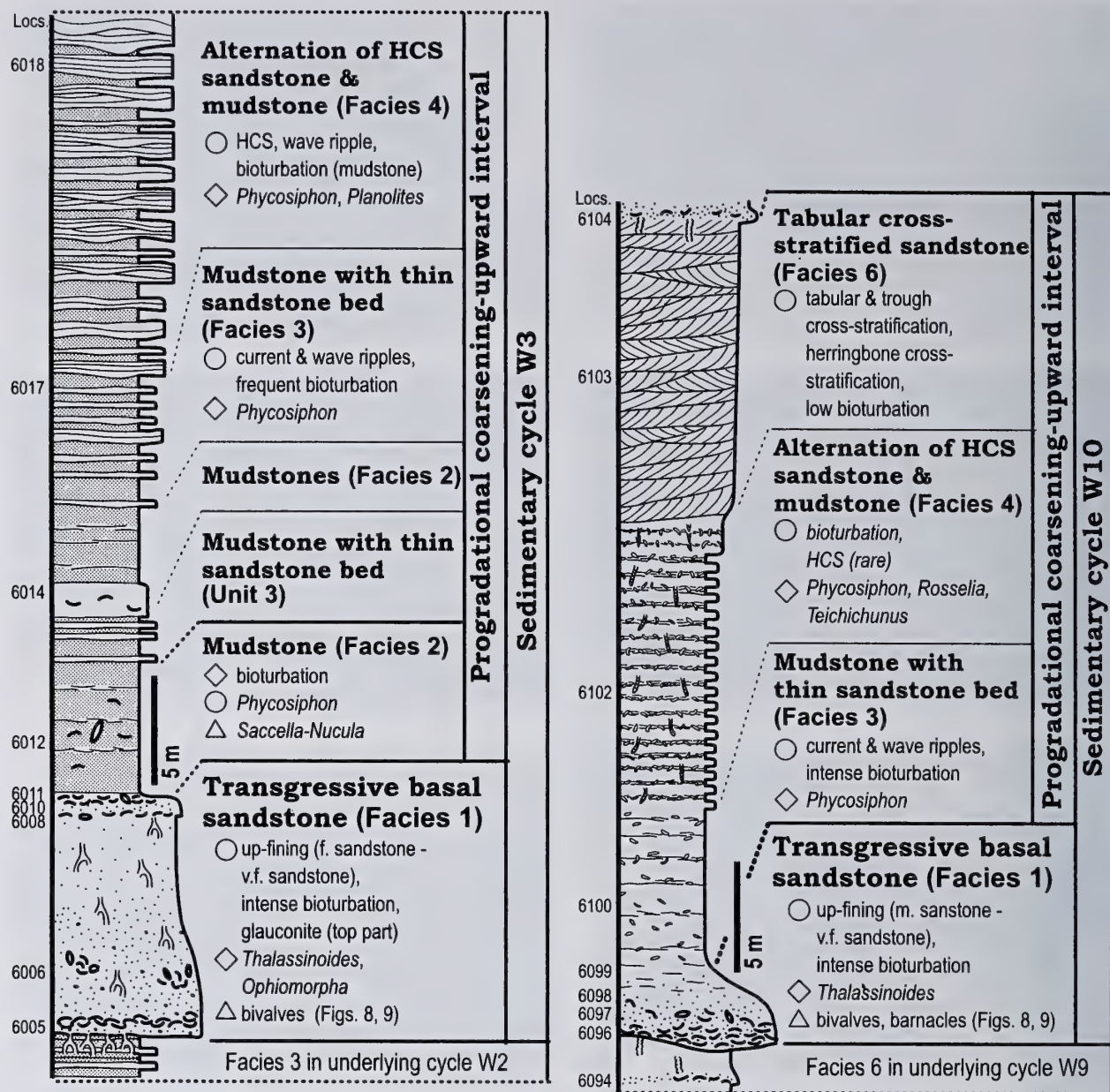


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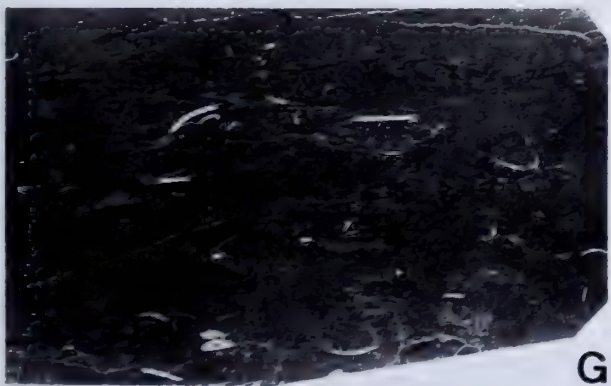
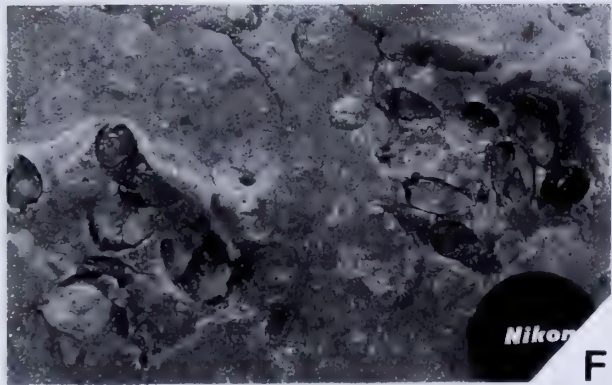
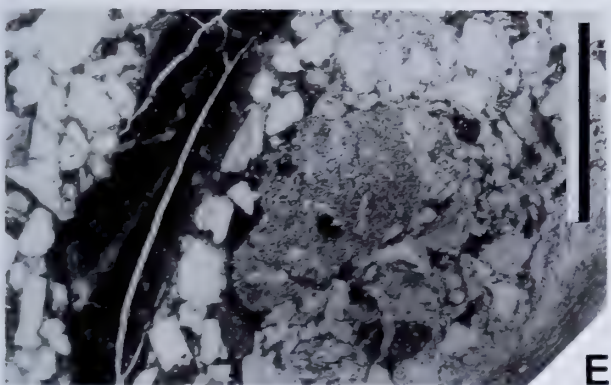
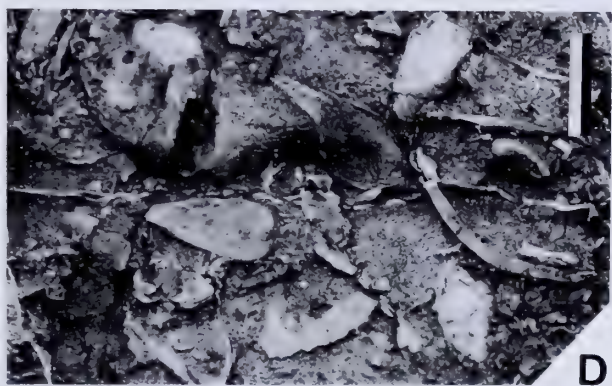
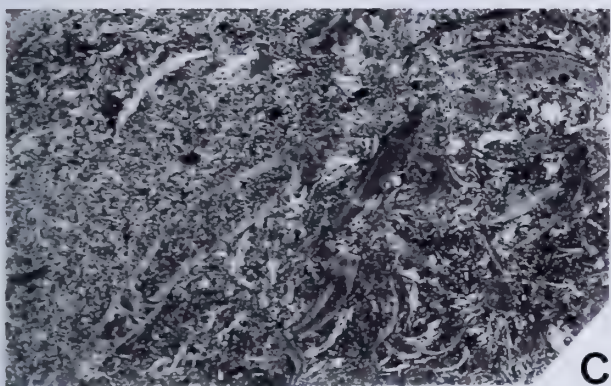
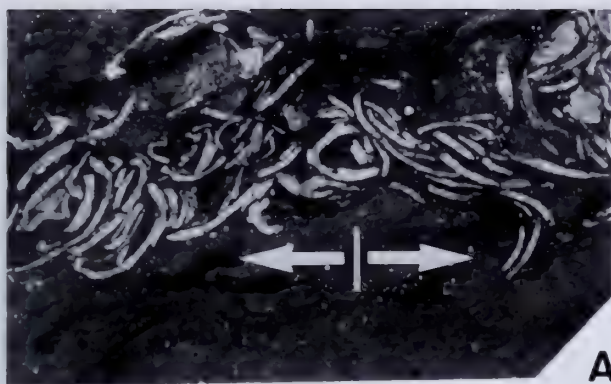




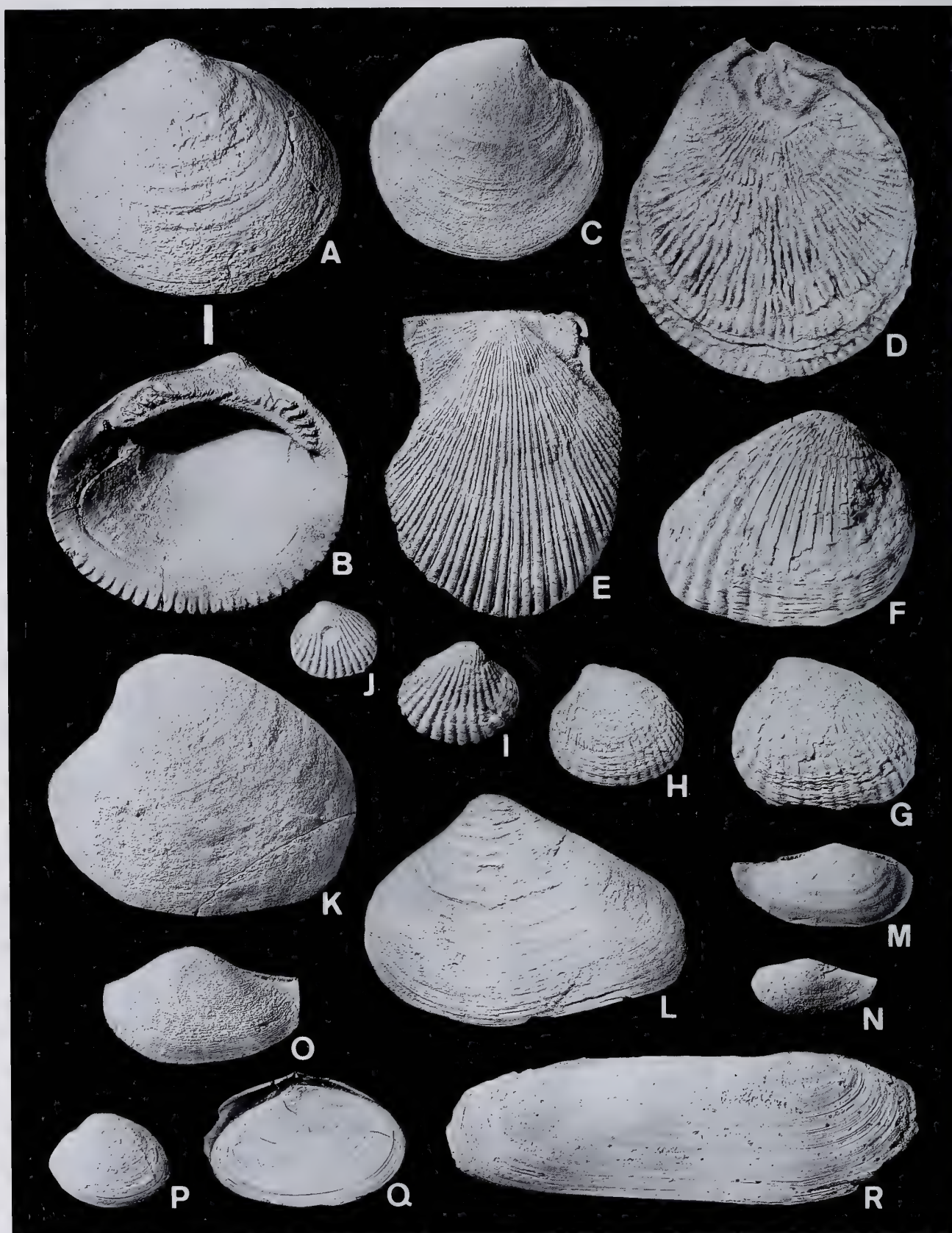
**Figure 5.** Sedimentary cycles and the lithological facies in the Waita Formation. Each cycle is subdivided into the basal sandstone (Facies 1) and the up-coarsening interval (Facies 2–5 or 6).

➔ **Figure 6.** Modes of fossil occurrence. **A.** Bidirectional imbrications (arrows) of shell fragments of the *Glycymeris-Phacosoma* Assemblage (a) in the basal sandstone (Facies 1) of cycle W3, at Loc. 6005. This sedimentary structure is characteristic of a wave dune. Scale bar is 2 cm long. **B.** Epifaunal bivalves, *Chlamys* sp. and barnacles of *Venericardia-Crassatella* Assemblage (b2) in the basal sandstone (Facies 1) of cycle W11, at Loc. 6109. Barnacles attach to shell surface. Lens cap is 5.5 cm in diameter. **C.** Matrix of the host sediment of the *Venericardia-Crassatella* Assemblage with abundant epifauna (b2; same as in figure 6B). The shell fragments are concentrated and imbricated in the vertical profile. (X 0.9). **D.** Articulated shells showing geopetal of the *Venericardia-Crassatella* Assemblage (b2; same as in figure 6B). Scale bar is 2 cm long. **E.** Shell replaced by clay minerals of the *Venericardia-Crassatella* Assemblage (b2) in the basal sandstone (Facies 1) of cycle W10, at Loc. 6098a. Scale bar is 1 mm long. **F.** Horizontal view of shell clumps (*Venericardia subnipponica*) of the *Venericardia* Assemblage in the middle part of the basal sandstone of cycle W3, at Loc. 4407. Articulated shells are observed. Lens cap is 5.5 cm in diameter. **G.** Profile of the matrix deposits of the *Yoldia-Nucula* Assemblage (d) in the mudstone of the cycle W2, at Loc. 6001a. (Natural size.) **H.** Apices-oriented shells on minor erosional surface of the *Yoldia-Nucula* Assemblage (d; same as in figure 6G). Lens cap is 5.5 cm in diameter. Loc. 6001a.











ice (Locs. 6006, 6082, 6098a; Figure 4D). In cycle W3, many glauconite grains occur, especially from the top part of the transgressive basal sandstone just below the mudstone of Facies (2) (Figures 4E, 5). The basal sandstone is mottled and intensely bioturbated; *Thalassinoides* and *Ophiomorpha* burrows are abundant (Figure 4C). The basal erosional surface is burrowed occasionally by these ichnospecies (Loc. 6005).

In addition to the basal surface, several minor erosional surfaces are recognized, usually within the lower part of the sandstone. These erosional surfaces undulate with relief of up to 30 cm, and are usually overlain by allochthonous shellbeds or pumice layers (Figures 4A, 5). The basal shellbed locally forms small shell mounds on the wavy erosional surface. These shells show bidirectional imbrications (Loc. 6005; Figure 6A). Such sedimentary structure characterizes a wave dune (Cheel and Leckie, 1992). Articulated bivalve shells are dispersed as patches in the upper part of the basal sandstone (Figures 5, 6F), in contrast to the allochthonous shellbeds in the lower part of the facies.

Molluscan fossils are abundant (Figure 7). Assemblages of (a) *Glycymeris-Phacosoma*, (b) *Venericardia-Crassatella*, and (c) *Venericardia* occur from this facies (Figure 8; described later).

#### Progradational coarsening-upward interval (Facies 2–6)

Two types of progradational coarsening-upward intervals are recognized in the Honjo and Waita Formations. The first type is composed of mudstone (Facies 2), mudstone interbedded with very thin sandstone beds (Facies 3), alternated HCS sandstone and mudstone (Facies 4), and amalgamated HCS sandstone (Facies 5) in ascending order. Another type of the coarsening-upward intervals is also composed of the Facies (2–4) capped by tabular cross-stratified sandstone (Facies 6). That is, Facies (6) replaces Facies (5) in the uppermost part of the interval. Facies (5) and (6) do not coexist within a single cycle.

**Mudstones (Facies 2).**—This facies conformably covers the basal sandstone (Facies 1), and characterizes the lowermost part of the progradational coarsening-upward interval (e.g., Cycle W3; Figure 5). It consists of dark gray laminated or bioturbated mudstone 5–40 m thick. Very fine sandstone beds (less than 5 cm thick) are occasionally intercalated in the mudstone (Locs. 4402, 6001a, 6050). *Yoldia-Nucula* Assemblage (Figure 8; described later) and

*Phycosiphon* ichnosp. are abundant in the bioturbated parts (Figure 6G).

**Mudstone interbedded with very thin sandstone beds (Facies 3).**—This facies changes transitionally from the underlying mudstone (Facies 2) (Loc. 6012 etc.), or directly covers the basal sandstone (Facies 1) (Locs. 6012 and 6100). It attains 3–10 m thickness (Locs. 4404, 6003, 6052 etc.), and is characterized by mudstone interbedded with very thin sandstone bed of less than 15 cm thickness. The sheet sandstone is very fine, and shows parallel, current and wave ripple laminations.

Primary sedimentary structures are sometimes disturbed by *Phycosiphon* ichnosp. (Figure 4F). The intensely bioturbated part which directly covers the basal sandstone yields various types of ichnofossils (*Planolites*, *Paleophycus*, *Rosselia*, *Skolithos* etc.; Locs. 6088, 6100), and molluscan fossils such as *Acila ashiyaensis* and *Dentalium* sp. etc. (Figure 8).

**Alternation of HCS sandstone and mudstone (Facies 4).**—This facies overlies Facies 3, and is capped with the Facies (5) or (6). It is 3–20 m thick and consists of alternations of sandstone and mudstone (Locs. 6017, 6047, 6101 etc.). The sandstone beds are 15–150 cm thick and tend to thicken upward, and each bed has a slight erosional base. Hummocky cross stratification, parallel lamination and wave ripples are well observed in the sandstone without remarkable signs of bioturbation. In contrast, the interbedded mudstone is commonly bioturbated by *Phycosiphon* ichnosp. (e.g., Cycle W3 at Loc. 6017). In Cycles W9 and W10, both sandstone and mudstone are exceptionally intensely bioturbated by *Phycosiphon* and *Planolites* ichnospp. (Locs. 6089, 6102; Figure 4G), and also yield *Teichichnus* and *Rosselia* ichnospp. *Rosselia* burrows show the upward removal trails to escape from rapid burial (Nara, 1997).

**Amalgamated HCS sandstone (Facies 5).**—This facies consists of amalgamated HCS sandstone, 10 m thick, at the top part of the cycle (Locs. 6026, 6048; Figure 4H). The sandstone is clean, well-sorted and very fine-grained. Primary sedimentary structures, such as hummocky cross-stratification, are well preserved. Mudstone and wave rippled sandstone beds, 20 cm thick, are rarely intercalated in the sandstone. The top of this facies yields many *Ophiomorpha* burrows (Loc. 6027).

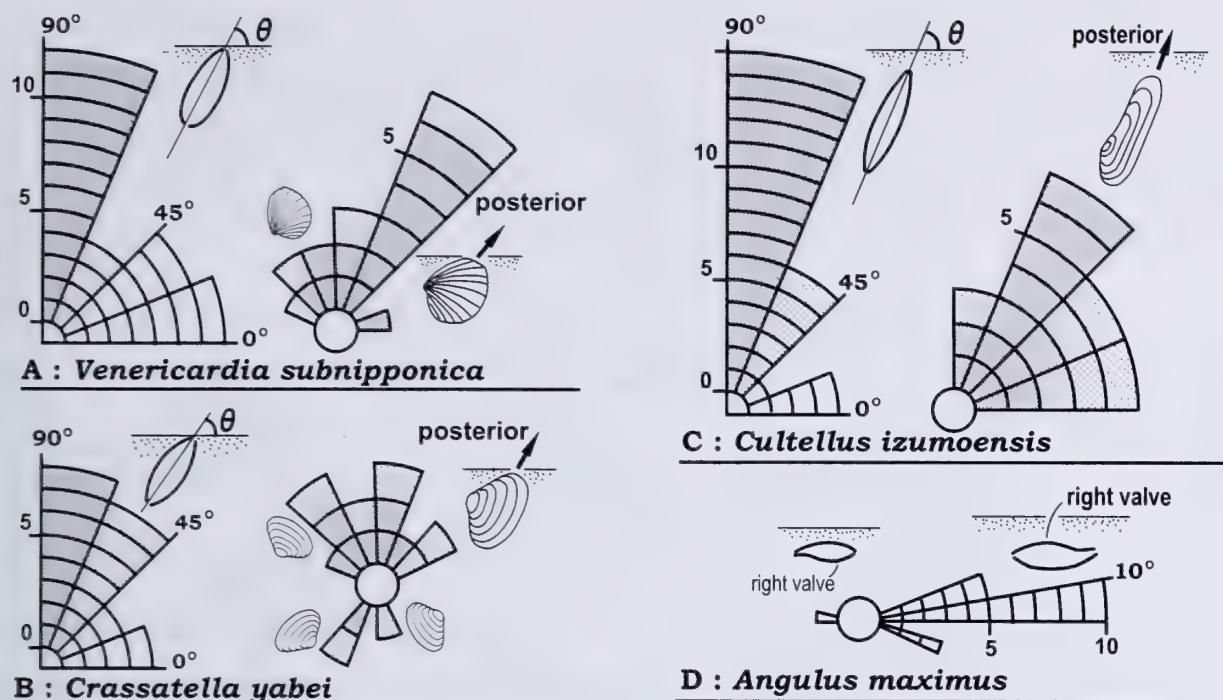
**Tabular cross-stratified sandstone (Facies 6).**—Some cycles have tabular cross-stratified sandstone (6) at the top,

← **Figure 7.** Bivalve fossils from the Waita Formation (D, R X0.9; I, M, O, Q X2; N X2.5; J, P X3; others X1). **A, B.** *Glycymeris cisshuensis* Makiyama, Cycle W5 at loc. 6043. **C.** *Phacosoma chikuzenensis* Nagao, Cycle W9 at loc. 6083. **D.** *Monia* sp., Cycle W3 at loc. 6008. **E.** *Chlamys* sp., Cycle W10 at loc. 6098a. **F–J.** *Venericardia subnipponica* Nagao, F, G, H; Cycle W1 at loc. 4309. I, J; Cycle W2 at loc. 6001a. **K.** *Pitar matsumotoi* (Nagao), Cycle W10 at loc. 6083. **L.** *Crassatella yabei* (Nagao), Cycle W5 at loc. 6043. **M, N.** *Yoldia* sp., Cycle W2 at loc. 6001a. **O.** *Sacculina* sp., Jinnobaru F. at loc. 3100. **P.** *Nucula* sp., Cycle W2 at loc. 6001a. **Q.** *Angulus maximus* (Nagao), Cycle W2 at loc. 6001a. **R.** *Cultellus izumoensis* (Yokoyama), Jinnobaru F. at loc. 3100. All specimens in this figure are housed in the Kyoto University Museum.

	Sedimentary cycle	Locality. no.	Bivalvia																			Gastropoda					others								
			<i>Glycymeris cishuensis</i>	<i>Phacosoma chikuzenensis</i>	<i>Pitar matsumotoi</i>	<i>Meretrix</i> sp.	<i>Spisula</i> sp.	<i>Crassostrea</i> sp.	<i>Crassatella yabei</i>	<i>Venericardia subnipponica</i>	<i>Chlamys</i> sp.	<i>Monia</i> sp.	<i>Arca sakamizuensis</i>	<i>Clinocardium</i> sp.	<i>Felaniella</i> sp.	<i>Lucinoma nagaioi</i>	<i>Cultellus izumoensis</i>	<i>Solamen subformicatum</i>	<i>Periplomya</i> sp.	<i>Angulus maximus</i>	<i>Saccula</i> sp.	<i>Yoldia</i> sp.	<i>Acila ashiyaensis</i>	<i>Nucula</i> sp.	"Diloma" sp.	<i>Phyllonoyus ashiyaensis</i>	<i>Euspira ashiyaensis</i>	<i>Turritella infralirata</i>	<i>Turritella karatsuensis</i>	<i>Fulgoraria</i> sp.	<i>Dentalium</i> sp.	barnacles	<i>Spatangoida</i>	<i>Echinodiscus ashiyaensis</i>	calcareous tube of <i>Serpulid</i> worm
W11	6109	12 5 4					25 (4)	2	27	29															5	2						15		2	2
W10	6098 a	5					33 (6)	37 (12)	31 (2)	8 (4)	2 (2)															4	4			2	2	15			
	6097	14 (2)	16				8	17																											
	6096	58 34					3	7	6																										
W9	6094		5																														6		
	6087																		2 (2)			36 (10)									6				
	6086							53 (8)								14 (8)				42 (2)	4	1	6												
	6083		54 12					26 (4)																								5			
	6082		25 (4)	18 (4)			27	11 (4)																											
W7	6062	10 12 2					8	23																											
W6	6049		5 (2)																																
W5	6043	72 12 2					14																					10							
	6027	6 26 15 1 4																								4									
W4	6022					15																													
W3	6014														10 (8)			10 (4)													12				
	6012														14 (8)			2 (2)		5		8								8					
	6011 a							98 (8)									9 (4)	4 (4)	7	10															
	6010 a		27 (4)	21 (8)			12 (4)	102 (8)	2	3		5	8							5								3							
	6008	3	9 (4)	15 (6)				73 (58)	1	9 (4)																		3	6						
	6006							72 (52)																											
	6005	36 33																																	
W2	6001 a						4 (2)							4 (2)	23 (22)			16 (10)		35 (8)	1	14				6		4		18					
W3	4407						87 (18)																												
	4406	36 55																																	
W2	4402						3								8 (8)			20 (12)		12 (4)	2	8						4		10					
W1b	4217						57 (4)							4 (4)														20		30					
	4315													10														2	34		90				
	4312			1				48 (20)																											
	4310 a							27 (12)							2 (2)	98 (80)											8	50		18	4	1			
	4309							77 (60)								2 (2)				6								2			2				
W1a	4308 a						14 (2)							1							42 (8)														
	4306																				5														

Figure 8. Fossil list in the Waita Formation (route map area). Numbers of articulated bivalve shells is parenthesized.





**Figure 9.** Diagrams showing orientation of articulated bivalve shells in outcrop. **A.** *Venericardia subnipponica* at Loc. 6097, **B.** *Crassatella yabei* at Loc. 6097, **C.** *Cultellus izumoensis* at Loc. 6001a, **D.** *Angulus maximus* (tellinid bivalve) at Loc. 6001a. Left diagrams in A-C show total modes of lateral inclination of commissure planes. Lateral inclinations MORE THAN 45° are stippled by dark or light. Right diagrams in A-C show posteriorward direction of selected specimens maintaining their standing positions in the left diagrams (lateral inclinations more than 45° are stippled samples of left diagrams). These articulated shells mainly are elevated in the posterior direction of shell length at angles of about 60°. Darkly or lightly stippled blocks correspond to those areas in left diagrams. D indicates dips of commissure planes and upper valve either left or right. Most articulated *Angulus maximus* lie keeping their right valve up.

instead of Facies (5). Facies (6) consists of tabular and trough cross-stratified fine sandstone 10–15 m thick. Single sets of tabular and trough cross-stratified beds range from 20 to 40 cm thick. Herringbone cross-bedding, tidal-bundle sequences and reactivation surfaces are well observed in the facies (Locs. 6060, 6092, 6102; Sakakura and Masuda, 2001). Lenticular and flaser bedding, 20–30 cm thick, is rarely intercalated in the tabular and trough cross-stratified sandstone (Loc. 6070). As in Facies (5), the top of this facies yields many *Ophiomorpha* burrows (Locs. 6094, 6104).

#### Interpretation of sedimentary environments

##### Sedimentary environments of transgressive basal sandstone (Facies 1)

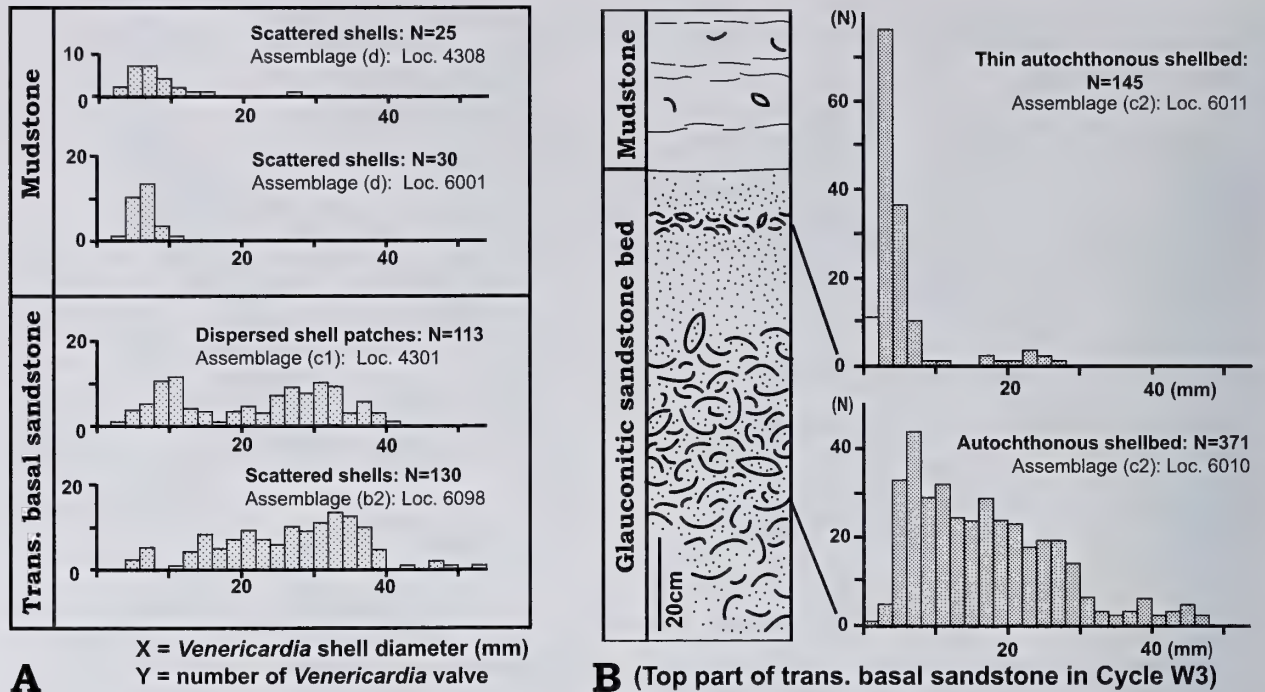
The transgressive basal sandstone can be interpreted as the deposits of relative sea level rises during transgression, because signs of wave influence clearly decrease upward. At the base of the basal sandstone (Facies 1), the wave dune is observed on the erosional surface. Such wave

dunes strongly suggest deposition under the intense influence of waves in shallow environments (Cheel and Leckie, 1992). No sedimentary structures formed by waves are observed in the upper part of the basal sandstone. Therefore, the upper part of this facies is interpreted to having been deposited below the storm wave base. The view is supported by the fining-upward features of these deposits and the bivalve assemblages whose contents and modes of occurrence differ clearly between the lower and upper parts (discussed later).

##### Sedimentary environments of coarsening-upward intervals (Facies 2–6)

*Progradation of wave-dominated shoreline (Facies 2–5).*—The progradational coarsening-upward intervals composed of Facies (2–5) shows wave-influenced sedimentary structures such as wave ripples and hummocky cross-stratification increasing upward.

Facies (2) is the lowermost part of this coarsening-upward interval, and shows no signs of wave-influenced sedimentary structures. It gradually changes upward into



**Figure 10.** A. Size distribution patterns of *Venericardia subnipponica* shells that occur as scattered shells or dispersed shell patches from the basal sandstone (Facies 1) and mudstone (Facies 2). In the basal sandstone, *Venericardia* shells vary in size from less than 10 mm diameter to up to 50 mm. The size-distributional patterns show wide level-curves rather than polymodal ones. In contrast, only small shells, less than 15 mm, occur from the overlying mudstone (Facies 2). B. Size-distribution patterns of *V. subnipponica* shells accumulated into autochthonous shellbeds at the top of the basal sandstone. The shell size-distribution pattern in the lower shellbed has a broad range from 2 mm to 48 mm and a gentle and inclined "peak" at 6–8 mm. In contrast, the pattern in the upper shellbed has a very strong mode at 2–4 mm for about 50% of the total number of valves, and with 85% concentrated in the 0–6 mm range.

the overlying Facies (3) in which wave ripple are observable. These features suggest that Facies (2) was deposited below the storm wave base in an outer shelf environment.

Facies (3) and (4) are usually intercalated between the hemipelagic Facies (2) and the amalgamated HCS sandstone (Facies 5). They are characterized by alternation of sandstones that exhibit wave ripples and hummocky cross-stratification, and mudstone. Hummocky cross-stratification is well known in episodic storm deposits (e.g. Dott, Jr. and Bourgeois, 1982). On the other hand, the mudstone represents hemipelagic deposition during fair-weather conditions. Thus, the alternation of sandstones and mudstone (Facies 3 and 4) may suggest deposition above storm wave base and below fair-weather wave base.

The amalgamated HCS sandstone (Facies 5) is the uppermost part of the coarsening-upward interval. This facies is characterized by amalgamated HCS sandstones with few intercalations of hemipelagic mudstone, and indicates deposition above fair-weather wave base. These characters of this facies are typically found in lower shoreface deposits (Walker and Plint, 1992).

The coarsening-upward interval composed of Facies

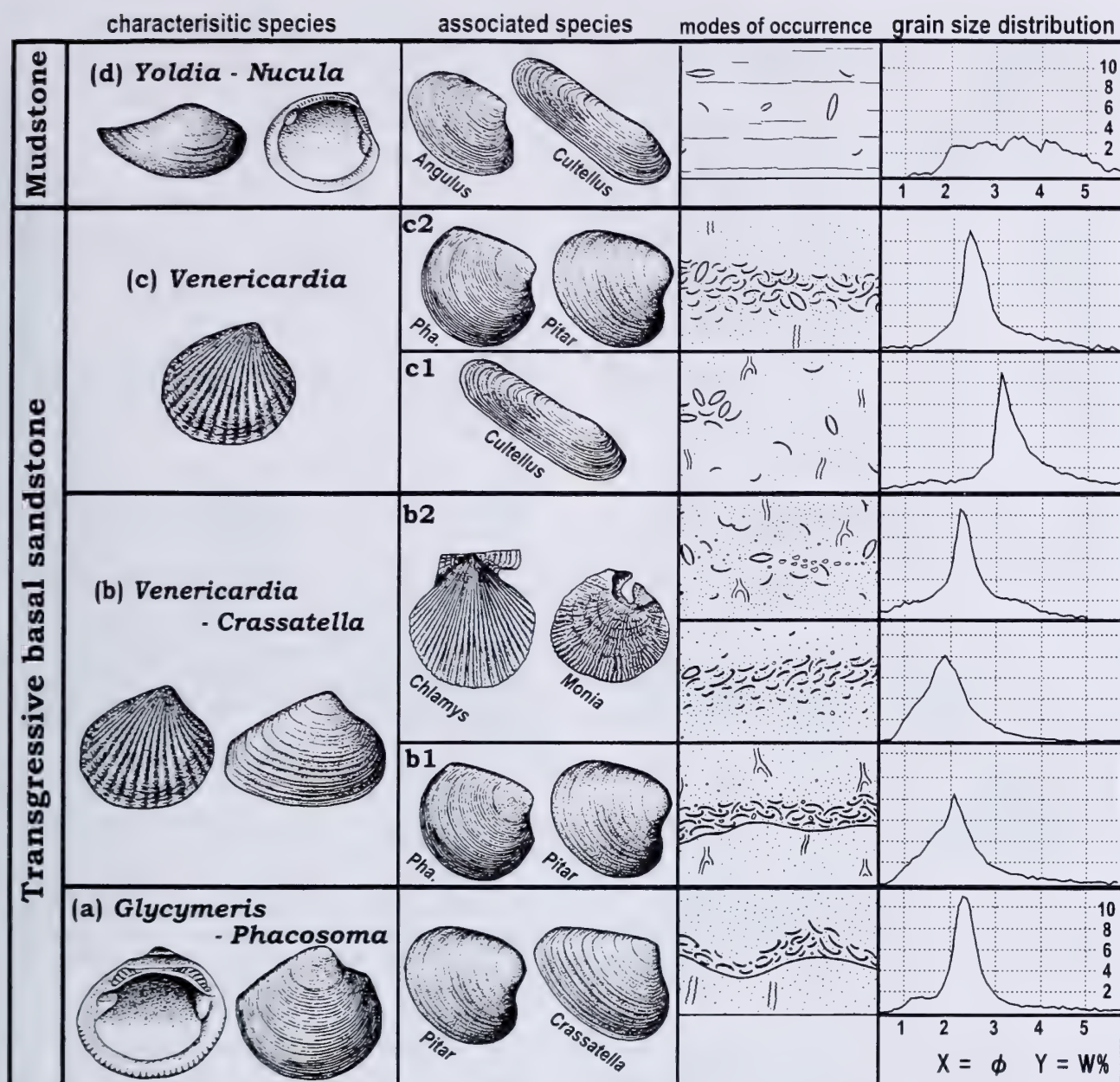
(2–5) may record a successional environmental change from below storm wave base to lower shore face. Such a successional change reflects the progradational processes of a wave-dominated shoreface (e.g., Walker and Plint, 1992).

*Progradation of a wave- and tide-influenced shoreline (Facies 2–4 and 6).*—Another coarsening-upward interval similarly consists of Facies (2–4) in its lower and middle parts. However, the uppermost part of the interval is replaced by the tabular cross-stratified sandstone (Facies 6), instead of amalgamated HCS sandstone (Facies 5).

The tabular cross-stratified sandstone (Facies 6) overlies inner shelf deposit (Facies 4) and exhibits many tide-influenced sedimentary structures such as herringbone cross-stratification, tidal-bundle sequences, reactivation surfaces, and lenticular and flaser bedding (Nio and Yang, 1989). Based on these features, Facies (6) is interpreted to have accumulated in subtidal or intertidal environments.

The progradational coarsening-upward interval with tidal deposits (Facies 6) at the top also reflects progradational process. In contrast to the coarsening-upward interval of a wave-dominated shoreface, however, it was deposited in a tide- and wave-influenced shelf. Such progradational



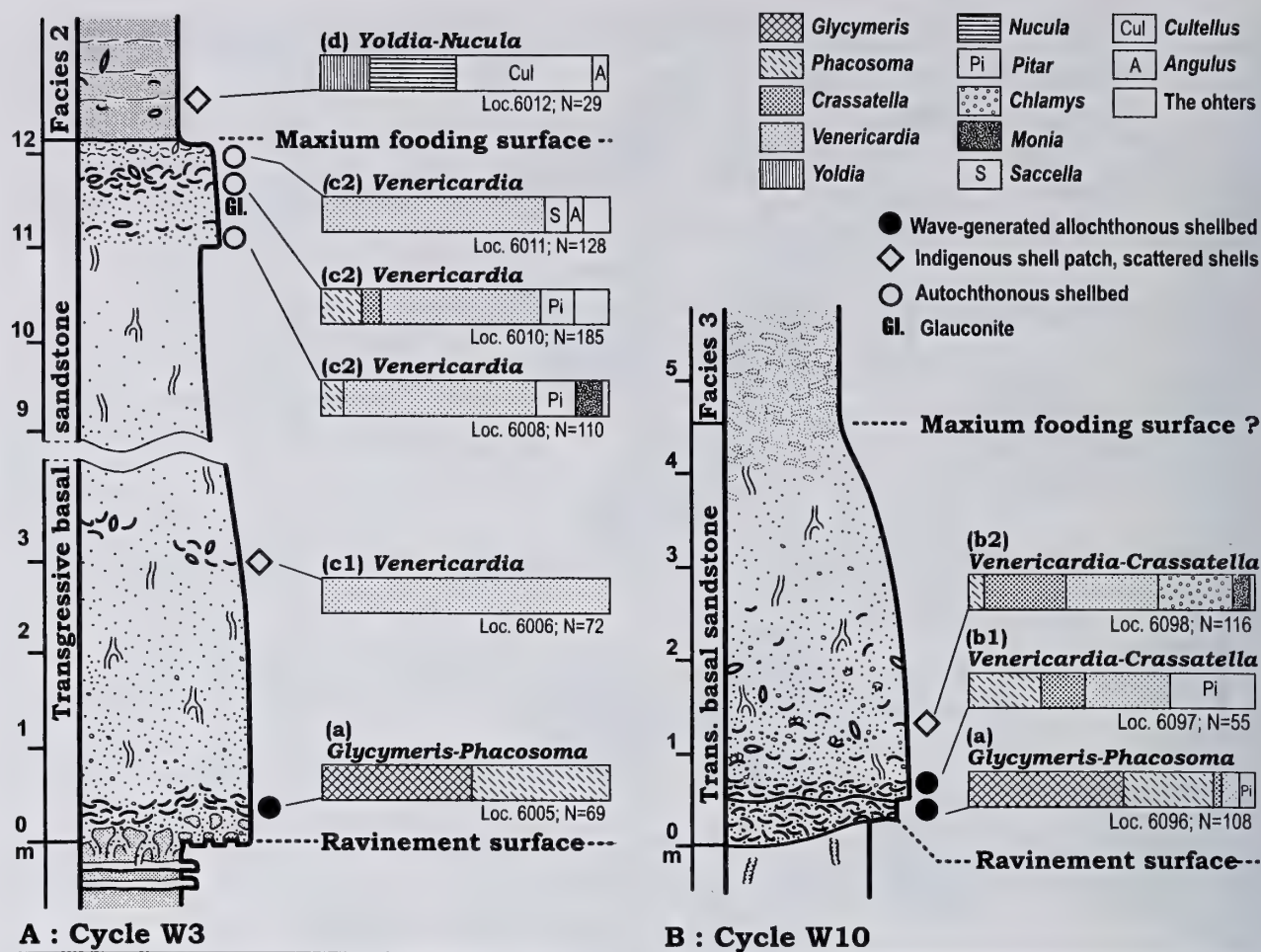


**Figure 11.** Schematic diagram of bivalve assemblages, showing their compositions, typical modes of occurrence and grain size distributions of the host sediments. The lowermost *Glycymeris*-*Phacosoma* Assemblage (a) occurs from the well-sorted medium-grained sandstone (Facies 1) as an allochthonous shellbed on the basal erosional surface. On the other hand, the *Yoldia*-*Nucula* Assemblage (d) indigenously occurs from poorly sorted siltstone (Facies 2). The *Venericardia*-*Crassatella* and *Venericardia* Assemblages (b, d) show intermediate taphonomic features between the erosional phase and the muddy quiet phase in each cycle.

deposits on a tide- and wave-influenced shelf was reported from the Devonian of the central Appalachian and upper Precambrian of Scotland (Prave *et al.*, 1996; Kessler and Gollop, 1988).

#### Meaning of redefined sedimentary cycle by sequence stratigraphy

After revision of the cycle boundaries, every cycle can be redefined as a pair of the transgressive basal sandstone that exhibits the decreasing of wave influence, and the progradational coarsening-upward interval of the regressive phase. The new definition seems quite consistent with a



**Figure 12.** Successive change of fossil bivalve composition in the transgressive basal sandstone (Facies 1) and the lower part of the overlying mudstone (Facies 2). A. Cycle W3 and B. Cycle W10 are the most typical examples. Four assemblages can be discriminated. *Glycymeris-Phacosoma* Assemblage (a) is replaced upward by the *Yoldia-Nucula* Assemblage (d) via the *Venericardia-Crassatella* (b) and *Venericardia* Assemblages (c). Although all of these assemblages are not always observable in a cycle, the successive change is widespread in every cycle in the Waita Formation.

framework of sequence stratigraphy. The basal sandstone and the coarsening-upward interval reflect the transgressive and high-stand systems tracts, respectively (Posamentier and Vail, 1988). The distinct erosional surface at the base of every cycle probably corresponds with the ravinement surface (transgressive surface; Swift, 1968; Nummedal and Swift 1987), and the glauconitic sandstone beds in the top part of the transgressive basal sandstone in the Cycle W3 (Figure 6E) is regarded probably as the condensed section (Loutit *et al.*, 1988) at maximum flooding surface, which is generated by low sediment supply and slow deposition. Revision of the sedimentary cycles provides a simple but more reasonable paleoenvironmental framework for further studies on paleoecology.

### Succession of molluscan assemblages

#### Molluscan assemblages

Molluscan fossils occur abundantly in, and are stratigraphically restricted to, the transgressive basal sandstone (Facies 1) and the overlying mudstone (Facies 2 and 3) in the lower part of each cycle (Figures 3, 5 and 7). Four different fossil assemblages are distinguished from the viewpoints of faunal composition and modes of occurrence. These four assemblages occur successively within a section, appear repeatedly in every cycle in the same order, and show characteristic taphonomic features. I have examined their modes of occurrence, paying particular attention to articulation and burial position of the shells, shell fabric and fragmentation in shellbeds, articulated bivalve fossils still in life position, and shell size distribution



(Figures 6, 9 and 10). Figure 11 summarizes the contents and modes of occurrence of the four assemblages. The grain size distribution of their host sediments was investigated in detail by a settling tube system. The settling distance was 150 cm, and the cumulative sediment weight was automatically logged by computer.

(a) *Glycymeris-Phacosoma* Assemblage.—This assemblage is characterized by *Glycymeris cisshuensis* and *Phacosoma chikuzenensis*, and is associated with *Pitar matsumotoi*, *Crassatella yabei* etc. (Figures 8, 11, 12).

The assemblage (a) characteristically occurs in clean sandstone, which rests directly on the erosional basement (ravinement surface) of the transgressive basal sandstone (Figure 12). The occurrence interval is 50–100 cm thick above the base. The host sandstone is massive or sometimes mottled by bioturbation (Figure 4C, D), and is fine- to medium-grained.

The shells are densely concentrated as an allochthonous shellbed of 20–50 cm thick, on an erosional surface at the base of the cycle (Locs. 6005, 6043, 6096; Figure 4A). The erosional surface shows wavy undulation, whose relief is up to 20 cm high. Bivalve shells are usually disarticulated and somewhat fragmented. They are sometimes piled up and imbricated bidirectionally along both slopes on the crest (Loc. 6005; Figure 6A). These features are characteristic of wave dunes (Cheel and Leckie, 1992).

The assemblage consists mainly of medium- to large-sized shells (30–100 mm). Their calcareous shell tests are occasionally replaced by clay minerals (Figure 6E).

A grain-size distributional pattern of the sandstone matrix is highly concentrated, and the mode lies on fine-grained sand size ( $\phi = 2.3$ ; Figure 11). Very fine sand or finer grains ( $\phi > 3$ ) do not contribute much (Figure 11).

(b) *Venericardia-Crassatella* Assemblage.—The assemblage consists mainly of *Venericardia subnipponica* and *Crassatella yabei* (Figures 11, 12). It is subdivided into two subtypes by differences of the associated species. The first subtype (b1) is associated with *Phacosoma chikuzenensis* and *Pitar matsumotoi* which are common in the *Glycymeris-Phacosoma* Assemblage (a) (Locs. 6082, 6097; Figures 8, 11, 12). The second subtype (b2) is characteristically associated with epibionts represented by epifaunal byssally attached bivalves, *Chlamys* sp. and *Monia* sp., and by barnacles, which attach to molluscan shell surfaces (Locs. 6098a and 6109; Figures 6B, 8, 11, 12).

The first subtype assemblage with *Phacosoma* and *Pitar* (b1) occurs from medium to fine-grained sandstone in the lower to middle parts of the transgressive basal sandstone (Figure 12). The shells occur as allochthonous shellbeds of 20 cm thick on wavy erosional surfaces (Locs. 6082, 6097 etc.), much as those of the *Glycymeris-Phacosoma* Assemblage (a). Green smectite and pumice grains are common in the sandstone. Grain-size distribution of the

sandstone matrix shows a moderately concentrated curve (Figure 11). The mode lies on fine-grained sand size ( $\phi = 2.2$ ). Silt-size or finer grains, less than 4  $\phi$  in diameter, do not amount to much.

The second subtype with epifaunal byssally attached bivalves (b2) occurs from medium to fine-grained sandstone 1–2 m thick in the middle part of the basal sandstone (Figure 12). The second subtype assemblage (b2) includes articulated individuals of *Venericardia subnipponica*, *Crassatella yabei* and *Chlamys* sp. (Figures 11, 12). The shells are scattered about the bioturbated sandstone which includes smectite and pumice grains, and which has also little silt or finer grains ( $\phi > 4$ ). The grain-size distributional pattern is similar to that of the first type (b1; Figure 11).

Articulated shells account for 32% of total *V. subnipponica* and 18% of total *C. yabei* shells (Loc. 6098a; Figure 8). Some of them are still in their living position. For example (see Figure 9), twelve among 29 articulated individuals of *V. subnipponica* stand with their commissure plane almost vertical. In this case, most of the standing ones raise their posterior part upward with angles around 60° (Loc. 6098c; Figure 9A). *C. yabei* also exhibits trend similar to that of *V. subnipponica* but the burial pattern is much more dispersed (Loc. 6098c; Figure 9B).

Some disarticulated and articulated bivalve shells are occasionally encrusted by barnacles. Epifaunal byssally attached bivalves such as *Chlamys* sp. and *Monia* sp. are typical examples. They are encrusted not only on the outer side of shells but also on the inner side (encrustation on the inner side indicates that it occurred after the death of the host bivalves). The barnacles keep their attaching colony on the encrusted shell, and the large barnacles shells are consecutively attached by small individuals of new generations. Barnacles also occur as dislocated colonies and disarticulated shell fragments.

The shells of the assemblage (b2) are sometimes accumulated as shellbeds, however, no erosional surface is observed at the base (Loc. 6109). The matrix of the shellbed consists of a mixture of many shell fragments showing imbrications, articulated shells filled by geopetal, and medium- to fine-grained sands (Figure 6C and D). Shell fragments are variously abraded (Figure 6C). Encrustation by barnacles is common on disarticulated bivalve shells (Figure 6B).

In both subtypes (b1 and b2), medium- and large-sized shells of *V. subnipponica* (20–40 mm) are abundant (Locs. 6083, 6095, 6098b). In contrast, small shells less than 10 mm in diameter are few. Figure 10A shows a size-distributional pattern of *V. subnipponica* shells that are scattered about the middle interval of the basal sandstone at Loc 6098b. The smaller-shell portion might have been trimmed off the original thanatocoenosis by fragmentation and winnowing out by wave currents or the replacement of



shell tests by clay minerals (Figure 6E).

(c) *Venericardia Assemblage*.—The assemblage is characterized by abundant *Venericardia subnipponica* (Figures 11, 12). The assemblage can be subdivided into two subtypes, c1 and c2, by difference of the associated species (Figure 11). The subtype (c1) consists mostly of *V. subnipponica*, and has very few associated species except for *Cultellus izumoensis* in places (Locs. 4310a, 4313, 6006 etc; Figures 8, 12). The subtype (c2) is characterized by a great quantity of *V. subnipponica*, and associated *Phacosoma chikuzenensis*, *Pitar matsumotoi*, *Monia* sp. and *Crassatella yabei* (Locs. 6009–6011a; Figures 8, 12).

The subtype (c1) occurs commonly from very fine sandstone 8–20 m thick in the middle to upper part of the transgressive basal sandstone (Figure 12). The sandstone yields many *Thalassinoides* burrows (Figure 4C). The *Venericardia* Assemblage (c1) occurs from much more fine-grained deposits than the assemblages (a) and (b). The grain-size distribution curve shifts fineward, and the mode lies on very fine sand size ( $\phi = 3$ ). Coarse and medium-grained sands are few.

The subtype (c1) occurs as indigenous shell-patches (Figure 11) or scattered shells. *Venericardia subnipponica* sometimes forms a shell clump composed of tens of articulated individuals (Locs. 4313, 6006; Figure 6F). They frequently keep their living position in bioturbated very fine sandstone. Size distribution pattern of *V. subnipponica* in the subtype (c1) has a wide range (4–40 mm) and polymodal curve (Loc. 4310b; Figure 10A). These features might result from overprinting of indistinguishable populations because of sampling from the thick interval of bioturbated and mottled sandstone.

On the other hand, Subassemblage (c2) is restrictedly found only from a glauconitic sandstone bed at the top of the transgressive basal sandstone in the cycle W3 (successive Locs. 6008, 6010a and 6011a; Figure 12). The shells of the Subtype (c2) accumulated as an autochthonous shellbed (Figures 10B, 11, 12), which contained articulated large *Monia* sp. that probably attached to other shells with a byssus, particularly in their early growth stage (Loc. 6008; Figure 7D). The grain-size distribution curve of the host rock has a mode at very fine sand ( $\phi = 2.4$ ; Loc. 6010a; Figure 11), which is slightly coarser than the host rock of the subtype (c1).

A great quantity of disarticulated *V. subnipponica* shells constructs a shellbed 40–60 cm in thickness (Loc. 6010b, Figure 10B). The shellbed starts with a gradual increase of shell content in the lower 20 cm interval, and ends at a sharp top. The shells are oriented at random, and are occasionally attacked by boring polychaetes. The shellbed also yields articulated individuals of *V. subnipponica* and *P. matsumotoi* (Figure 8), some still in their living positions. A quantity of *V. subnipponica* shells has a broad range in

shell diameter from less than 2 mm to 48 mm. The histogram of the shell size distribution shows a mode at 6–8 mm for 44 valves of 317; it forms a broad and inclined “peak” that rises swiftly from the smallest shells then declines gradually to the largest ones (Figure 10B lower).

In the transitional zone from glauconitic sandstone to mudstone (Facies 2), the subtype (c2) is composed particularly of many small *V. subnipponica* shells accompanied with *Angulus maximus*, an associated species of the *Yoldia-Nucula* Assemblage (d) at Loc. 6011a (discussed below; Figures 8, 12). Many small *V. subnipponica* shells are concentrated into a thin shellbed 2–5 cm in thickness. The histogram of the shell diameter distribution shows a high mode at the 2–4 mm; range, in which about 50% of the total of 145 valves are included. More than 85% of the valves fall in the range of 0–6 mm, and otherwise medium-sized shells (10–30 mm) account for only about 7% (Loc. 6011b; Figure 10B). A similar distributional tendency of *V. subnipponica* shell diameters is represented in the *Yoldia-Nucula* Assemblage (d) (described immediately below).

(d) *Yoldia-Nucula Assemblage*.—The assemblage consists mainly of *Yoldia* sp., *Nucula* sp., *Angulus maximus*, *Cultellus izumoensis*, *Venericardia subnipponica*, *Dentalium* sp. (Locs. 6001a and 6012; Figures 8, 11, 12). Unlike the other assemblages, the *Yoldia-Nucula* assemblage occurs from the bioturbated mudstone (Facies 2; Figure 6G) which overlays the basal sandstone (Facies 1) at Locs. 4308a and 6012 (Figure 10), and the grain size distributional pattern shows a broad curve extending from fine sand size ( $\phi = 2$ ) to silt size ( $\phi = 5$ ; Figure 11) without an obvious peak.

Usually, the molluscan fossils are scattered about the mudstone (Figure 6G). Some bivalve shells of *Yoldia* sp. and *Nucula* sp. are articulated and arranged at random. Most *Cultellus izumoensis* shells are articulated (Loc. 6001a; Figure 8). Among 26 articulated individuals, fifteen *C. izumoensis* stand with their commissure plane subvertical, and frequently the posterior part is raised upward at angles around 60° (Loc. 6001c; Figure 9C). The shells of *Angulus maximus* (= tellinid bivalve) are also articulated in high numbers (Loc. 6001a; Figure 8), and retain their living position, in which their right-warped siphonal gape is oriented upward. Their articulated shells lie horizontally in the matrix still keeping their right valve uppermost. (Loc. 6001c; Figure 9D).

Shells of *Dentalium* sp. and *Turritella karatsuensis* occur occasionally as allochthonous shell stringers (Kidwell *et al.*, 1986) on minor erosional surfaces (Loc. 6001a). The horn- or drill-shaped shells are concentrated in parallel and arranged into a scar 50 cm long and 20 cm wide, and their apices are unimodally pointed (Figure 6H).

*Venericardia subnipponica* occurs not only from the basal sandstone (Facies 1) but also from the mudstone



(Facies 2). In the *Yoldia-Nucula* Assemblage (d), *V. subnipponica* is a subordinate species, and is represented only by small individuals. It accounts only for 4.1% of in total 97 individuals in the assemblage (b) at Loc. 6001a (Figure 8). Figure 10A show two shell diameter distributional histograms at localities 6001b and 4308b. The pattern at Loc. 6001b has a mode at 6–8 mm, and shells larger than 12 mm diameter are scarce.

#### Successive occurrences of molluscan assemblages

The molluscan assemblages change successively in upward sequence within the transgressive basal sandstone and the overlying mudstone in each cycle. The successive occurrences are similarly made up of, in ascending order, the (a) *Glycymeris-Phacosoma* Assemblage, (b) *Venericardia-Crassatella* Assemblage, (c) *Venericardia* Assemblage and (d) *Yoldia-Nucula* Assemblage (Figure 11). Their successive occurrence is never reversed in order, and is uniformly repeated in every sedimentary cycle, though all the four assemblages are not always completely observable within a cycle. Related to the faunal change, their typical modes of occurrence shift upward from allochthonous shellbed into indigenous shell clumps and patches.

The most typical examples of the Cycles W3 and W10 are summarized in Figure 12. In cycle W3 (Locs. 6005–6012; Figure 12A), the faunal succession starts with the *Glycymeris-Phacosoma* Assemblage (a), which occurs only as the basal allochthonous shellbed with wave dunes at the base of the cycle (Locs. 6005). The *Venericardia-Crassatella* Assemblage (b) is skipped there. The lowermost assemblage (a) is replaced upward directly by the *Venericardia* Assemblage (c) at the 3 m-level above the base. The top part of the occurrence range of the assemblage (c) intercalates with *V. subnipponica* shellbeds in glauconitic sandstone bed that indicates the surface of maximum transgression (11–12 m level in figure 12A). The shellbeds also yield a few *Phacosoma chikuzenensis* and *Pitar matsumotoi*, both of which are associate species of the Subassemblage (c2). The indigenous *Yoldia-Nucula* Assemblage (d) appears at the 12.5 m-level as the lithology changes quickly from sandstone to the overlying mudstone (Facies 2).

The faunal succession is almost identical in the Cycle W10, but is condensed within a thin basal interval (0–2 m level in Figure 12B). The *Glycymeris-Phacosoma* Assemblage (a) is also dominant on the basal erosional surface, and is similarly replaced upward by the *Venericardia-Crassatella* Assemblage (b1) on the erosional surface at the level of 0.5 m above the base (Loc. 6096–6097; Figure 12B). The latter assemblage (b1) is immediately succeeded by another subtype (b2) of the *Venericardia-Crassatella* Assemblage with abundant epibionts, such as *Chlamys* sp., *Monia* sp. and barnacles, at the level of 0.7 m

above the base (Loc. 6097, 6098a; Figure 12B). The occurrence range of Assemblage (b2) encompasses 1.5 m in thickness, and is terminated with an increase of mud content in the host rock (Figure 12B).

#### Discussion

##### Taphonomic implication of faunal change in cycles

Molluscan fossils mostly occur from the lower part of each cycle, i.e., the transgressive basal sandstone (Facies 1) and the mudstone (Facies 2) that had been deposited during the earliest regressive phase (Figure 12). Four distinctive fossil assemblages are preserved in this relatively thin part. Close taphonomical observation can “decode” the hidden paleoenvironmental and paleoecological changes condensed in this transgressive interval in high resolution.

The lowermost *Glycymeris-Phacosoma* Assemblage (a) occurs only as allochthonous shellbeds on the erosional base of the transgressive basal sandstone (Figures 11, 12). Most of the shells are disarticulated completely and fragmented considerably there, and often form wave dunes (Cheel and Leckie, 1992; Figure 6A). The matrix of the host rock is well-sorted, fine-grained sandstone, and the mud content is small (Figure 11). These features strongly suggest deposition under intensely wave-influenced conditions, in which the sea bottom is frequently eroded and shells are easily winnowed. The molluscan shells in this assemblage might be reworked repeatedly even if they were not transported horizontally far from their habitats. The succeeding *Venericardia-Crassatella* Assemblage associated with *Phacosoma* and *Pitar* (b1) occurs also as wave-influenced shellbeds on additional minor erosional surfaces (Figure 11).

In contrast, no signs of bottom erosion and shell reworking by wave currents are observable in the upper part of Facies (1) and, also in Facies (2). The *Venericardia* Assemblage (c) consists partly of autochthonous or indigenous shell patches, in the upper part of the basal sandstone (Facies 1), whose grain size distributional pattern shifts fineward ( $\phi > 3$ ; Figure 11).

The uppermost *Yoldia-Nucula* Assemblage (d) occurs mostly as indigenous scattered shells in the overlying mudstone (Facies 2; Figure 12). Their shells are often articulated and found in their living positions (Figure 10). These are no signs of bottom erosion and shell reworking. The host rock contains very fine sand ( $2 < \phi < 3$ ) but is dominated by muds (Figure 11). Allochthonous shells of *Dentalium* sp. and *Turritella karatsuensis* are sometimes accumulated in depressions on the bedding plane of the mudstone, and show preferred orientation (Facies 2; Figure 6H). The cause of such apex-oriented shell stringers is not attributable to waves but to unidirectional currents (Nagle, 1967; Figure 6H).



The successional change of these taphonomic features suggests that the faunal succession is closely associated with the upward decreasing of wave influence. The *Glycymeris-Phacosoma* Assemblage (a) is replaced upward by the *Yoldia-Nucula* Assemblage (d) via the *Venericardia-Crassatella* and *Venericardia* Assemblages (b, c), while the strong wave influence declines from the erosional and winnowing phase to the quiet muddy phase through the transgression period.

Successive faunal change within a sedimentary cycle is widespread and exhibited repeatedly in the Waita Formation. The *Glycymeris-Phacosoma* Assemblage always occurs as the allochthonous shellbed, which corresponds to an onlap shellbed (Kidwell, 1991) on the ravinement surface that indicates early transgression. The other assemblages also retain the autochthonous or indigenous occurrences above this onlap shellbed. Besides the Ashiya Group, similar faunal change in and above onlap shellbeds is observable in the other Paleogene deposits (e.g., the Nishisonogi Group and Hioki Group). Therefore, it seems one of the basic sedimentological and paleoecological features of the Paleogene deposits in west Japan.

#### Epibionts-enriched fauna

The successive faunal records are sometimes condensed within a very short interval in a cycle, for example, within an interval of 2 m thick from the base in the cycle W10 (Figure 12). Intermittent and limited deposition of this interval is suggested by abundant occurrence of epibionts. Epifaunal byssally attached bivalves: *Chlamys* sp. and *Monia* sp., and barnacles occur commonly as associated species of the *Venericardia-Crassatella* Assemblage (b) from the lower middle part of the transgressive basal sandstone (Figure 12). Some of them are found in the attaching position *in situ* (Figure 6B), while others are fragmented, abraded, and finally assimilated into the shellbed matrices showing imbrications (Figure 6C). Scarcity of fine-grained sediments in the matrix also implies that this component was winnowed out and swept away by currents (Subassemblage b2; Figure 11).

These epifaunal byssally attached bivalves and barnacles require the peculiar condition that their attachment to shelly ground avoids burial by the winnowing out of sediments. A number of shells have been attached by plural generations of barnacles (Loc. 6098a). Some other shells have repeatedly settled by epibionts after death. *Chlamys* and *Monia* probably attached to other shells by their byssus at least in the early ontogenetic stage, although the attachment position is not observable in the fossil record since the byssus is missing. The line of evidence converges to an argument that the shelly ground, which lifts the restriction on the migration of the epibionts, was exposed for a long

time. The signs of taphonomic feedback, by which the skeletal remains of dead organisms impact on the next living community (Kidwell and Jablonski 1983), are observable in places (Locs. 6008, 6098a and 6109). The epifaunal byssally attached bivalves cannot survive on the seafloor in which sediments are rapidly and continuously deposited; the same is true of the cemented barnacles, because they have neither a foot to escape rapid burial nor a siphon (Stanley, 1970; Kranz, 1974). The epibiont-rich shellbeds at least in three cycles might indicate strong or gentle current-influenced conditions in which sedimentation was intermittent, and probably, relatively slow.

#### Autochthonous shellbed in glauconitic sandstone

The glauconitic sandstone bed at the top of the transgressive basal sandstone intercalates with autochthonous shellbeds composed of a great quantity of *Venericardia subnipponica* shells (Subassemblage c2; Locs. 6010 and 6011). Unlike the allochthonous shellbed on the ravinement surface at the base of the cycle, the shellbed at the top is autochthonous because bivalve fossils often keep their living position (Figures 10B, 12). Abundant glauconite grains in matrices (Figure 4E), which develop in areas characterized by low sedimentation (Chamley, 1989), imply condensation as a process of shell accumulation *in situ* during a relatively long period. This view is also supported by the occurrence of epifaunal byssally attached bivalves such as *Monia* sp.

The shell diameter distributional pattern of *V. subnipponica* in this shellbed is shown in Figure 10B (lower). These shells range in length from 2 to 48 mm, with a low mode at 6–8 mm. This may suggest a continuous and stable supply of dead shells of all growth stages *in situ*, which consist of many juveniles and a few mature specimens, except for very small juveniles that have little fossilization potential. As noted above in the sequence stratigraphic interpretation of the sedimentary cycle, the glauconitic sandstone where the autochthonous shellbed lies is regarded as a condensed section associated with the maximum-flooding surface (Figures 5, 12B).

The autochthonous shellbed in the glauconitic sandstone probably reflects attrition from a normal population or "cemetery" (Ager, 1963; Dodd and Stanton, Jr., 1990). It is produced by repetitive colonization of *Venericardia subnipponica* populations *in situ* under low sedimentation rate during the maximum-flooding period. Such a shellbed at the top of a transgressive deposit is classified as a backlap shellbed by Kidwell (1991).

On the other hand, another autochthonous shellbed is intercalated in the transitional zone from the glauconitic sandstone to overlying mudstone (Facies 2) (Figure 10B, upper).

It is composed mostly of small shells of *Venericardia*



*subnipponica*, some of which are articulated (Figure 10B). In contrast to the *Venericardia* Assemblage in the glauconitic sandstone, the size-distributional pattern of the present species shifts strongly to the smallest portion (Figure 10B upper). The mode of the histogram lies at 2–4 mm, in which more than 50% of the total individuals are concentrated. These features probably suggest that a mass mortality of juvenile shells occurred after an opportunistic larval settlement, and that these shells represent a census population (Ager, 1963; Dot and Stanton Jr., 1990).

*Venericardia* is a typical infaunal nonsiphonate suspension feeder having limited mantle fusion. They are usually shallow and slow burrowers (Stanley, 1970), and have low escape ability from rapid burial (Kranz, 1974). Consequently, the mass mortality may be involved with the incidental deposition of soupy muds that caused an obrution. The population of *Venericardia* juveniles might be smothered by the obrution event in the transitional phase between condensed glauconitic and muddy. It should be noted that *Venericardia* populations in the overlying mudstone (Facies 2; *Yoldia-Nucula* Assemblage) are also restricted to small-diameter shells.

### Conclusion

Based on detailed observations, 11 sedimentary cycles in the upper part of the Ashiya Group (upper Oligocene) were revised and redefined here (Figure 5). Each cycle consists of a basal erosional surface overlain by a transgressive basal sandstone and a progradational-interval of mudstones and sandstones. In this revision, every cycle is bordered by an erosional surface at the base of a fossiliferous sandstone. Four molluscan fossil assemblages are distinguished. They exhibit similar successive occurrences accompanied with transitions of sedimentological and taphonomical features. These are a key to understanding the Paleogene stratigraphy and paleoecology, because similar successive occurrences of bivalve fossils are widespread in other Paleogene deposits in western Japan (i.e., Nishisonogi and Hioki Groups). The successive occurrence of bivalve fossil faunas is interpreted to result from transgressive-regressive shifts in sedimentary regimes (variable wave influence and sediment supply).

Paleoecological aspects of Paleogene bivalves, for example *Venericardia*, still remain obscure. Unlike Neogene or Quaternary fauna, direct analogies from the ecology of modern relatives should not be simply drawn for Paleogene bivalves. On the other hand, taphonomic and sedimentologic aspects can be directly read from the strata. Sedimentary regime seems to be a factor in defining the habitats of bivalves, and is regarded as the most important environmental factor controlling morphologic adaptations of bivalves (Stanley, 1970), owing to their benthic habitat,

which not only is closely related to the depositional substrate, but also contains many infaunal styles of burrowing into deposits. Therefore, taphonomic and sedimentologic observation will be a key to understanding the paleoecology of Paleogene bivalve fauna.

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## SHORT NOTES

# Revision of an Ordovician cephalopod *Ormoceras yokoyamai* (Kobayashi, 1927)

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## Introduction

Systematic position of an Ordovician cephalopod *Ormoceras yokoyamai* (Kobayashi, 1927) is reconsidered on the basis of type specimens kept in the University Museum of the University of Tokyo (prefixed UMUT) and the new material from the type stratum Jigunsan Formation, Choson Supergroup in Gangwon-Do, South Korea. The Jigunsan Formation, named by Yamanari (1926), is a relatively thin (45–100 m in thickness) fossiliferous sequence of interbedded shale and subordinate limestone. On the basis of studies primarily of trilobites and cephalopods, Kobayashi (1966) assigns the principal part of the formation to Llanvirn (upper Middle Ordovician). This correlation is in agreement with conodont biochronology by Lee (1977, 1980). The newly collected specimens come from float blocks of shale at (1) locality G90075, latitude 37° 10' 39.5'' N, longitude 128° 42' 7.1'' E, in a field on the southwestern slope of Mt. Jigun, Jikdongri, Jungdong-myeon, Yeongwol-gun (UMUT PM 27827), and (2) locality J89105, latitude 37° 5' 42.4'' N, longitude 129° 0' 52.6'' E, on the northern flank of a small tributary of the Hwangji River in Jangseong, Taebaek-city (UMUT PM 27828).

## Systematic paleontology

- ? Subclass Actinoceratoidea Teichert, 1933
- ? Order Actinocerida Teichert, 1933
- Family Proteoceratidae Flower, 1962
- Genus *Treptoceras* Flower, 1942

*Type species.*—*Orthoceras duseri* Hall and Whitfield, 1875.

*Treptoceras yokoyamai* (Kobayashi, 1927)

Figure 1

*Loxoceras yokoyamai* Kobayashi, 1927, p. 186, 187, pl. 18, figs. 9a–c.

*Sactoceras yokoyamai* (Kobayashi). Kobayashi, 1934, p. 439, 440, pl. 27, figs. 1–6, pl. 28, fig. 2.

*Ormoceras yokoyamai* (Kobayashi). Yun, 1999, p. 214.

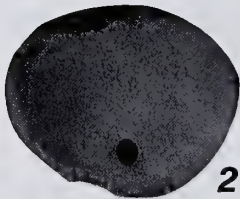
*Emended diagnosis.*—Small species of *Treptoceras* with low angle (approximately 5°) of shell expansion, oval cross section with form ratio (lateral/dorsoventral diameter) 1.2–1.5; siphuncle submarginal with siphuncular position ratio (minimum distance of central axis of siphuncle from shell wall per dorsoventral shell diameter) approximately 0.2 in adoral shell; septal necks cyrtchoanitic to suborthochaoanitic; cameral deposits weak for genus.

*Description.*—Small-sized orthocones for genus with gradual shell expansion indicating approximately 5° in dorsoventral plane (Figure 1.1); apical shell may be curved on the basis of a specimen (UMUT PM 0686 figured by Kobayashi, 1934, pl. 27, fig. 6); details of shell surface not observed in all examined specimens, but annulations and conspicuous ornamentation not detected; cross section of shell dorsoventrally depressed, oval with form ratio of 1.2–1.5 (Figure 1.2); largest known specimen (UMUT PM 0685 figured by Kobayashi, 1934, pl. 27, figs. 3–5) attains 11.0 mm in dorsoventral diameter and 15.5 mm in lateral diameter, whose adoral part represents apical body chamber; sutures transverse to slightly oblique, nearly straight or weakly sinuate to form very shallow ventral and dorsal lobes in rare cases (Figure 1.1); camerae very short, giving width/length ratios which ranges from 4.6 to 10.9+, with shallow septal curvature (Figure 1.3); no septal furrow detected; adoral siphuncle stenosphonate and submarginal in position, with siphuncular position ratio approximately 0.2 (Figure 1.3); septal necks cyrtchoanitic to suborthochaoanitic, not recumbent (Figure 1.4–1.7); well-preserved dorsal septal neck attains 0.27 mm in length at dorsoventral shell diameter of approximately 7 mm; adnation area usually





1



2



3

ed



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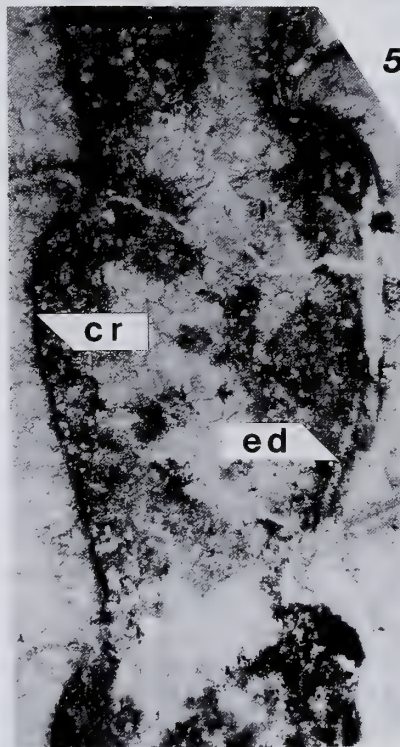
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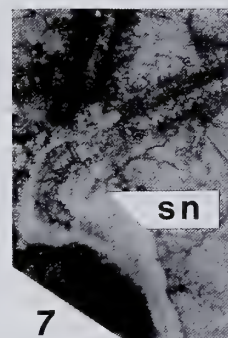
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8

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absent; connecting rings relatively thick, 0.05–0.07 mm, and undifferentiated (Figure 1.5), forming subglobular profile in apical dorsoventral section of a specimen (UMUT PM 0686) with maximum diameter/length ratio of siphuncular segments approximately 1.3, inflation then rapidly decreases, creating fusiform to pyriform (and subglobular in rare cases) profile in adoral dorsoventral section with ditto ratio 0.6–0.9 (Figure 1.4, 1.5); curvature of septal brims and inflation of connecting rings are slightly stronger on ventral siphuncular side than on dorsal one (Figure 1.4, 1.5); cameral deposits weak for genus, restricted in apical camerae, composed of thin episeptal-mural and hyposeptal deposits (Figure 1.3). Endosiphuncular deposits are also restricted to apical siphuncle (Figure 1.3); laminated parietal deposits to form thick lining on ventral siphuncular wall (Figure 1.4, 1.6); thickness of ventral lining decreases at septal foramen and its surface usually linear in profile in longitudinal section (Figure 1.4, 1.6); parietal deposits rarely developed on dorsal connecting rings, which interrupted at septal foramen (Figure 1.4); canal system and perispatium not developed.

**Discussion.**—Morphologically, the most diagnostic feature of this species is the structure of the endosiphuncular deposits that is observable in Kobayashi's specimen UMUT PM 0687 (Figure 1.8), and a section from the new material, UMUT PM 27827 (Figure 1.3–1.6). Its combination of the characteristic parietal deposits that form the ventral lining and lack of a canal system (Figure 1.4, 1.6) confirm systematic placement of the species in the Proteoceratidae rather than the Pseudactinoceratidae (*Loxoceras* M'Coy, 1844; Doguzhaeva and Shkolin, 1999) or the Ormoceratidae (*Ormoceras* Stokes, 1840 and its subjective junior synonym *Sactoceras* Hyatt, 1884). In addition, the species does not exhibit an exogastric cyrtcone, surface annulations and strongly bulging sutural elements, which features are diagnostic only for two closely related genera, i.e., *Treptoceras* (some emendations to the generic diagnosis were added by Aronoff, 1979, and Frey, 1988) and *Proteoceras* (Flower, 1955; type species *Ooceras*(?) *perkinsi* Ruedemann, 1906). These genera can be distinguished by the degree of the siphuncular changes which are less drastic in *Treptoceras duseri* and the present Korean species (Figure 1.3) than in *Proteoceras perkinsi*. The siphuncular segments of *Proteoceras* shift from a subglobular form to a nearly cylindrical one in the space of 6–8 camerae. Accordingly, *Ormoceras yokoyamai* is attributed to *Treptoceras*.

Although confident determination of the proteoceratid's

higher taxonomic position is pending until the apical shell form is clarified, it is herein proposed that a possible origin of the Proteoceratidae was derived from the subclass Actinocerida. Flower (1962) placed the Proteoceratidae in the order Orthocerida of the subclass Nautiloidea, and his assertion was followed in the Treatise (Sweet, 1964) and by Aronoff (1979) and Frey (1988). However, the rapid decrease of the siphuncular inflation of *Proteoceras perkinsi*, *Treptoceras duseri*, and *T. yokoyamai* is exceedingly unusual for the subclass Nautiloidea, and it seems rather suggestive of a phylogenetic relationship with some actinocerids including *Paractinoceras* (Hyatt in Zittel, 1900), *Leurorthoceras* (Foerste, 1921) and *Kobayashiceras* (Niko, 1998). Endosiphuncular lining deposits lacking radial canal and perispatium are also known in the adoral siphuncle of *Kobayashiceras*. This indicates that presence or absence of the canal system in the adoral shell is not always essential for Actinoceratoidea.

**Material examined.**—The holotype, UMUT PM 0016. The five specimens, UMUT PM 0683–0687, also identified as this species by Kobayashi (1934). In addition, the two new specimens of the imperfect phragmocones of UMUT PM 27827, 44.8 mm in length, and UMUT PM 27828, approximately 31 mm in length, have been examined.

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◀ **Figure 1.** *Treptoceras yokoyamai* (Kobayashi). 1, 3–7. UMUT PM 27827. 1, dorsal view,  $\times 8$ ; 3, dorsoventral thin section, venter on right,  $\times 8$ ; 4, details of apical siphuncle,  $\times 30$ ; 5, details of adoral siphuncle,  $\times 30$ ; 6, details of endosiphuncular deposits,  $\times 50$ ; 7, details of adoral septal neck,  $\times 50$ . 2. UMUT PM 27828, septal view of adoral end, venter down, silicon rubber replica,  $\times 4$ . 8. UMUT PM 0687, dorsoventral polished section, venter on right,  $\times 5.5$ . Abbreviations: **cr**, connecting ring; **ed**, endosiphuncular deposits; **sn**, septal neck.

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◎2002年年会・総会は2002年6月21日（金）、22日（土）、23日（日）の3日間にわたり福井県立恐竜博物館（福井県勝山市）で開催されます。6月21日（金）には国際シンポジウム「環日本海地域における白亜系層序と国際対比 ―手取層群を中心として―：世話人、平野弘道・長谷川卓・佐野晋一・東洋一」が開催されます。また、総会と懇親会はシンポジウムに続いて開催します。一般講演の申し込み締切は2002年5月7日（火）です。

◎第152回例会は2003年1月25日（土）、26日（日）に横浜国立大学教育人間科学部にて開催の予定です。

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### CONTENTS

#### ARTICLES

- Gengo Tanaka, Koji Seto, Takao Mukuda and Yusuke Nakano:** Middle Miocene ostracods from the Fujina Formation, Shimane Prefecture, Southwest Japan and their paleoenvironmental significance ..... 1
- Rodolfo Dino and Geoffrey Playford:** Stratigraphic and palaeoenvironmental significance of a Pennsylvanian (Upper Carboniferous) palynoflora from the Piauí Formation, Parnaíba Basin, northeastern Brazil ..... 23
- Dhurjati Prasad Sengupta:** Indian metoposaurid amphibians revised ..... 41
- Keiji Nakazawa:** Permian bivalves from the H. S. Lee Formation, Malaysia ..... 67
- Yutaro Suzuki:** Systematic position and palaeoecology of a cavity-dwelling trilobite, *Ityophorus undulatus* Warburg, 1925, from the Upper Ordovician Boda Limestone, Sweden ..... 73
- Moriaki Yasuhara, Toshiaki Irizuki, Shusaku Yoshikawa and Futoshi Nanayama:** Changes in Holocene ostracode faunas and depositional environments in the Kitan Strait, southwestern Japan ..... 85
- Norihiko Sakakura:** Taphonomy of the bivalve assemblages in the upper part of the Paleogene Ashiya Group, southwestern Japan ..... 101

#### SHORT NOTES

- Shuji Niko:** Revision of an Ordovician cephalopod *Ormoceras yokoyamai* (Kobayashi, 1927) ..... 121



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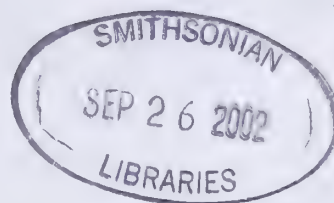


# Molluscan fauna of the “Miocene” Maéjima Formation in Maéjima Island, Okayama Prefecture, southwest Japan

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**Abstract.** Molluscan fauna of the “Miocene” Maéjima Formation is examined from taxonomical, biostratigraphical and paleozoogeographical points of view. It is composed of four gastropods and 14 bivalves including a new species. Two assemblages, the *Isognomon* and the *Megangulus-Acila* assemblage, were discriminated. The *Isognomon* assemblage is autochthonous or para-autochthonous and is composed of elements inhabited the littoral to upper sublittoral gravelly to rocky bottom in a warm sea. The *Megangulus-Acila* assemblage represents a mixed composition between muddy sand and gravelly to rocky bottom elements, and was formed in an upper sublittoral muddy bottom near a rocky shore. Occurrences of *Megangulus maximus* (Nagao), *Isognomon (Hippochaeta) hataii* Noda and Furuichi and *Chlamys (Leochlamys) namigataensis* (Ozaki) indicate the age of the Maéjima Formation as the Paleogene, not the Miocene. The molluscan fauna of the Paleogene Maéjima Formation contains both Tethyan Indo-Pacific elements and Northern Pacific elements. Taxonomy of selected molluscan taxa including a new arcid, *Arca (Arca) uedai* sp. nov., is described or discussed.

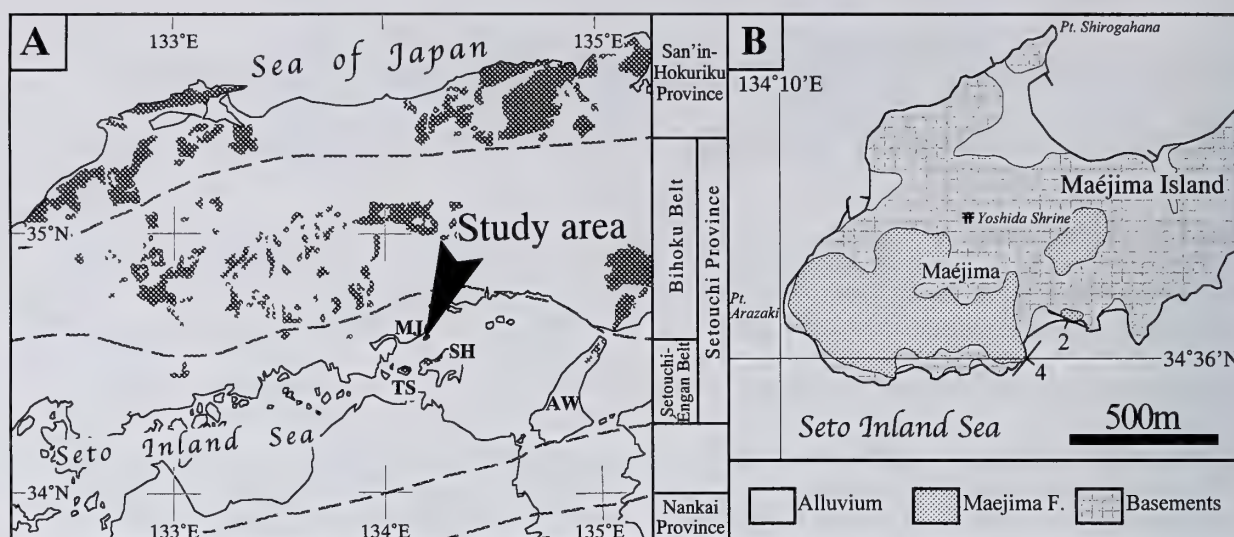
**Key words:** *Arca (Arca) uedai* sp. nov., First Setouchi Series, Maéjima Formation, molluscan fauna, Paleogene

## Introduction

The First Setouchi (or Setouti) Series (Kasama and Huzita, 1957) is the generic name for the Miocene strata scattered in the median zone of southwestern Japan (or the Setouchi Geologic Province; Ikebe, 1957), and all of its constituent formations had been regarded as uppermost lower to lower middle Miocene mainly on the basis of the lithology, sedimentary cycle and molluscs (e.g. Huzita, 1962; Itoigawa and Shibata, 1973, 1986, 1992; Ishida, 1979). It has been known that the “Miocene” molluscan assemblages in the coastal area of the eastern Seto Inland Sea (= Setouchi-Éngan Belt; Yano *et al.*, 1995a) are different from those in the neighboring backbone area (= Bihoku Belt; Yano *et al.*, 1995a), both in the western Setouchi Geologic Province (e.g. Huzita, 1962; Itoigawa, 1969, 1971, 1983; Ueda, 1991; Yano *et al.*, 1995a). There are two current interpretations explaining this difference; some paleontologists have postulated the existences of different water masses in the two areas in the late early to early middle Miocene (e.g. Itoigawa, 1983), while others have assumed a paleogeographic barrier between the two areas in the late early to early middle Miocene except during times of maximum transgression (e.g. Ueda, 1991; Takayasu

*et al.*, 1992; Yano *et al.*, 1995a).

On the other hand, it is becoming clear that constituent formations of the First Setouchi Series around the eastern part of the Seto Inland Sea are of Eocene to Oligocene, not Miocene age, as a result of studies during the last fifteen years (Matsuo, 1987; Ozaki and Matsuura, 1988; Suzuki *et al.*, 1995; Ozaki *et al.*, 1996; Yamamoto *et al.*, 2000b; Kurita *et al.*, 2000, 2001). Yamamoto *et al.* (2000b) found latest middle to late Eocene calcareous nannofossils and dinoflagellate cysts from the “Miocene” Iwaya Formation of the Kobe Group in Awajishima Island, and considered that the difference between the “Miocene” molluscan assemblages in the coastal area of the eastern Seto Inland Sea and those from the backbone area in the western Setouchi Geologic Province is due to chronologic difference. However, their opinion conflicts with the previous molluscan data because the Miocene species have often been listed from the First Setouchi Series in the eastern part of the Seto Inland Sea (Huzita, 1962; Saito, 1962; Saito *et al.*, 1970; Bando and Furuichi, 1978; Itoigawa, 1983; Huzita and Maeda, 1984; Mizuno *et al.*, 1990; Okumura and Sato, 1999). However, most of these studies are unaccompanied by either figures or descriptions of molluscan taxa. Thus, it is necessary to reinvestigate the molluscan



**Figure 1.** Location and geologic maps of the study area. **A.** Location of study area (arrow) and distribution of the "Miocene" sediments (hatched area; modified from Shibata and Itoigawa, 1980). The geologic province division follows Yano *et al.* (1995a) partly modified after Seto *et al.* (2000). AW: Awajishima Island, MJ: Maéjima Island, SH: Shodoshima Island, TS: Teshima Island. **B.** Geologic map of the western part of Maéjima Island, Okayama Prefecture.

fauna of the area, especially from the taxonomical point of view.

The Maéjima Formation is the Tertiary in the western part of Maéjima Island, Ushimado Town, Oku County, southeastern Okayama Prefecture (Figure 1A, B), and has been regarded as one of the constituents of the Miocene First Setouchi Series (e.g. Itoigawa, 1969, 1983; Itoigawa and Shibata, 1986). The distribution of the Tertiary in this island was for the first time reported by Sato (1938), and the stratigraphy was established recently by Yamamoto (2001). Although molluscan assemblages resembling those from other "Miocene" formations in the coastal areas in the eastern part of the Seto Inland Sea have been reported by Itoigawa (1969, 1971, 1983) and Yamamoto (2001) provisionally, precise constituents and faunal characteristics still remain unclear. In this paper, I taxonomically review the molluscan fauna of the "Miocene" Maéjima Formation and discuss the geologic age and its paleogeographical and paleozoogeographical implications.

### Geological setting

The Maéjima Formation (Itoigawa and Shibata, 1986, as Maeshima Formation; revised by Yamamoto, 2001) is distributed in the southwestern part of Maéjima Island, unconformably overlying the pre-Tertiary plutonic rocks (Figures 1B, 2). Although Yamamoto (2001) subdivided the Maéjima Formation into the Lower Conglomerate and Sandstone and the Upper Sandstone Member, they are

treated herein as the lower and the upper part with a revision of the boundary (Figure 2A).

The lower part of the Maéjima Formation is less than 10 m in thickness and is composed mainly of granule to pebble conglomerate with numerous fragments of balanids, brachiopods, calcareous algae and molluscs. This part is well exposed on the southwestern coast of Maéjima Island, which is designated to be the type locality of the formation.

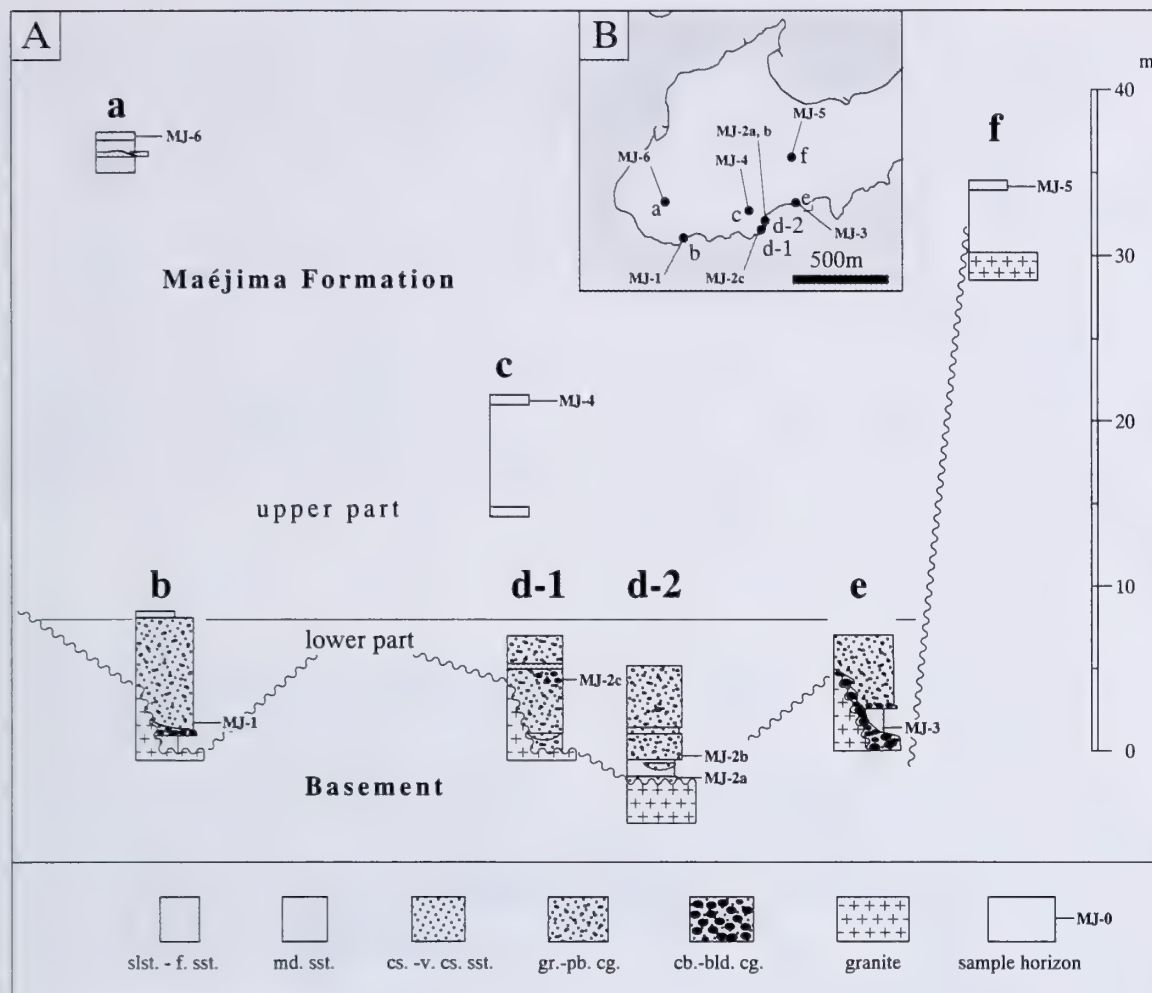
The upper part (30 m+) consists mainly of siltstone to muddy very fine-grained sandstone and is associated with calcareous medium- to coarse-grained sandstone. The upper part abuts on the basement and is conformably underlain by the lower part. Outcrop of the upper part is little exposed because it is distributed only in the hilly area with a low relief.

The age of the Maéjima Formation is not known precisely, which indicates an age of Yamamoto *et al.* (2000a) preliminarily reported a Sr isotope value of about 0.7077, which indicates an age of late Eocene or older.

### Material

Molluscan samples were collected from eight localities; five from the lower part and three from the upper part (Figure 2A, B). The preservation of fossil molluscs is quite poor and shell material of most specimens examined was dissolved away except for pectinids and an ostreid. Thus, hydrophilic vinyl polysiloxane impression materials (PROVIL novo, Putty®, regular set, Heraeus Kulzer, Inc.,





**Figure 2.** Columnar sections of the Maéjima Formation and locations of measured points and fossil localities. **A.** Columnar sections of the Maéjima Formation. Abbreviations. silt.: siltstone; sst.: sandstone (f.: fine-grained; m.: medium-grained; cs.: coarse-grained; v.cs.: very coarse-grained); cg.: conglomerate (gr.: granule; pb.: pebble; cb.: cobble; bld.: boulder). **B.** Map showing the points where the geologic columns (a through f) were made and fossil localities. Mapped area same as Figure 1B.

Ltd. and EXAFINE® Putty Type, GC Co., Ltd.) were used for the examination of molds.

### Molluscan fauna

Four species of Gastropoda and 14 species of Bivalvia including a new species were discriminated as a result of the examination (Table 1). On the basis of the dominant and associated species, the following two assemblages are discriminated (Figure 3).

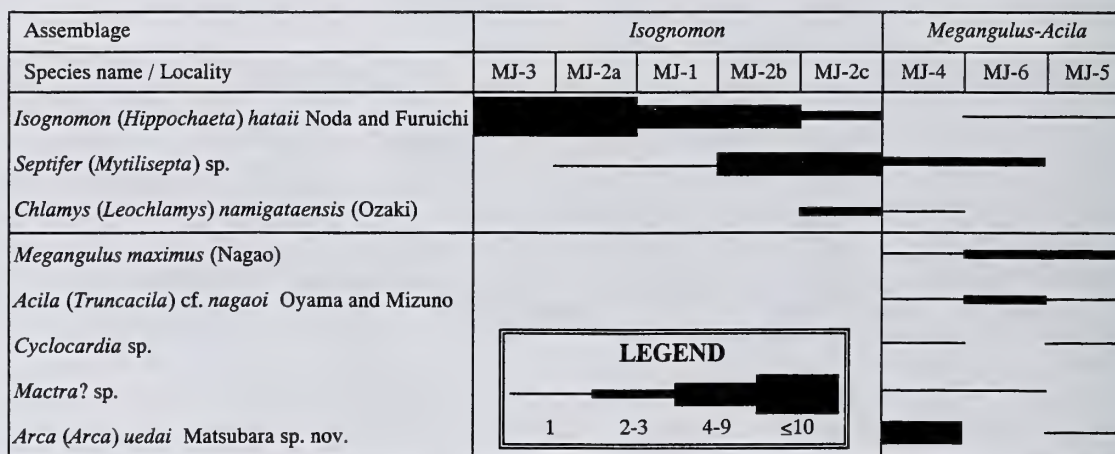
#### A. *Isognomon* assemblage

This assemblage is characterized by an abundant occurrence of *Isognomon* (*Hippochaeta*) *hataii* Noda and Furuichi, and is generally associated with a few specimens

of *Septifer* (*Mytilisepta*) sp. The *Isognomon* assemblage occurred from conglomerate to conglomeratic sandstone in the lower part of the Maéjima Formation (Locs. MJ-1, 2a, 2b, 2c and 3). At Loc. 3, *I. (H.) hataii* occurs abundantly in the matrix of boulder conglomerate without any associated species, and most of the specimens are articulated. At other localities, although most specimens of this species are disarticulated, they are less broken and a few articulated valves are included. Consequently, this assemblage is regarded to be autochthonous or para-autochthonous in broad sense. Taking the lithology of rocks in which the assemblage occurs and the habitat of the Recent homologues of these two species into account (Higo *et al.*, 1999), this assemblage inhabited littoral to upper sublittoral, gravelly to rocky bottom of an open sea.

**Table 1.** List of fossil Mollusca from the "Miocene" Maéjima Formation.

Horizon Species name/Locality	Lower part					Upper part		
	MJ-1	MJ-2a	MJ-2b	MJ-2c	MJ-3	MJ-4	MJ-5	MJ-6
<b>Gastropoda</b>								
Patellogastropoda, fam., gen. et sp. indet.								1
<i>Calyptrea</i> sp.						2		1
Naticidae? gen. et sp. indet.								1
Muricidae? gen. et sp. indet.						1		
<b>Bivalvia</b>								
<i>Acila</i> ( <i>Truncacila</i> ) cf. <i>nagaoi</i> Oyama and Mizuno						1	1	2
<i>Arca</i> ( <i>Arca</i> ) <i>uedai</i> sp. nov.						6	1	
<i>Glycymeris</i> ( <i>glycymeris</i> ) sp.								1
<i>Septifer</i> ( <i>Mytilisepta</i> ) sp.	1	1	3	4		2		2
<i>Isognomon</i> ( <i>Hippochaeta</i> ) <i>hataii</i> Noda and Furuichi	6	12	4	2	26		1	1
<i>Delectopecten</i> sp.								1
<i>Chlamys</i> ( <i>leochlamys</i> ) <i>namigataensis</i> (Ozaki)				2		1		
<i>Crassastrea</i> sp.			1					
Luchinidae gen. et sp. indet.						1		1
<i>Cyclocardin</i> sp.						1	1	
<i>Glans</i> sp.								2
<i>Megangulus maximus</i> (Nagano)						1	3	3
<i>Mactra</i> ? sp.						1		3
<i>Tapes</i> ? sp.								2
<b>TOTAL</b>	<b>7</b>	<b>13</b>	<b>8</b>	<b>8</b>	<b>26</b>	<b>17</b>	<b>7</b>	<b>21</b>

**Figure 3.** Molluscan assemblages of the Maéjima Formation. Number in legend indicates that of individuals.

The *Ostrea-Balanus* assemblage of Itoigawa (1969) probably corresponds to the *Isognomon* assemblage. But only a single specimen of *Crassostrea* sp. was collected from Loc. MJ-2c among all the localities examined in the present study. Consequently, the occurrence of the *Ostrea-Balanus* Assemblage from the Maéjima Formation is not supported.

#### B. *Megangulus-Acila* assemblage

The *Megangulus-Acila* assemblage occurred from siltstone to medium-grained sandstone in the upper part of

the Maéjima Formation (Locs. MJ-4, 5 and 6). This assemblage is characterized by infaunal Bivalvia species, *Megangulus maximus* (Nagao) and *Acila* (*Truncacila*) cf. *nagaoi* Oyama and Mizuno. Most shells of these species are disarticulated and are arranged parallel to the bedding plane. However, a few articulated specimens of *M. maximus*, *A. (T.)* cf. *nagaoi*, *Cyclocardia* sp. and *Mactra* ? sp. are recognized. This fact indicates that most shells of these species have not been transported a great distance from their original habitat. These species are regarded as shallow burrowers in an upper sublittoral, muddy to sandy



bottom (Higo *et al.*, 1999). On the other hand, *Arca* (*Arca*) *uedai* sp. nov., *Septifer* (*Mytilisepta*) sp. and *Isognomon* (*Hippochaeta*) *hataii* are considered to be epibyssate benthos on a gravelly to rocky bottom. There are no articulated specimens among these species, and thus they are considered to have been transported from their original habitat. These facts suggest that this assemblage represents a mixed composition formed in an upper sublittoral, muddy to muddy sand bottom neighboring a rocky shore in an open sea.

The occurrences of muddy to sandy bottom elements such as *Acila* (*Truncacila*), *Mactra*? and *Cyclocardia* indicate that this assemblage is compared with the *Mactra*-*Acila* assemblage of Itoigawa (1983) characterizing the molluscan assemblages in the coastal area of the eastern Seto Inland Sea.

### Discussion

#### Geologic age

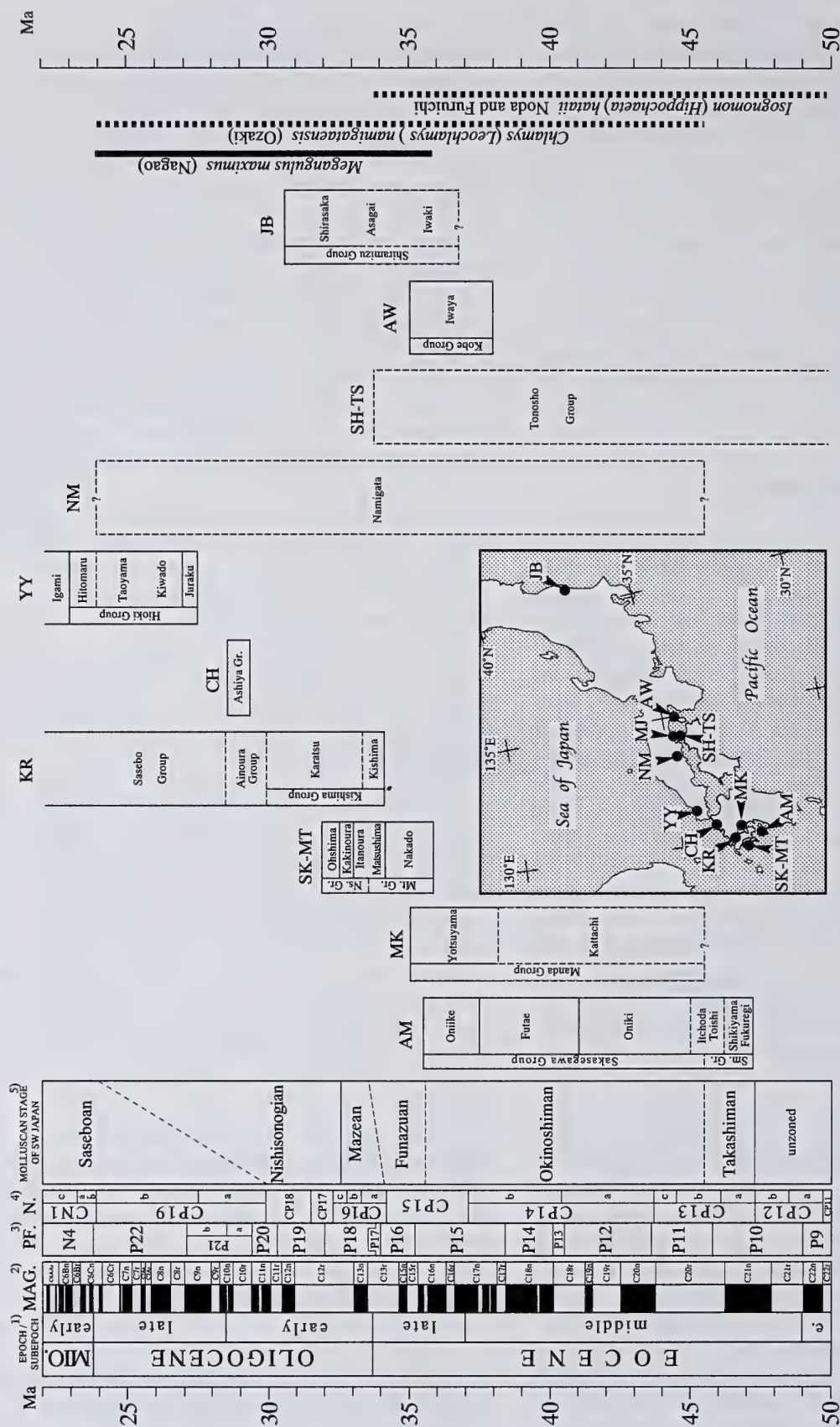
Among the constituents of the molluscan fauna of the Maéjima Formation, *Megangulus maximus* (Nagao), *Isognomon* (*Hippochaeta*) *hataii* Noda and Furuichi, and *Chlamys* (*Leochlamys*) *namigataensis* (Ozaki) are important for the age estimation (Figure 4). The first species has been recorded from the Paleogene of Kyushu and the other two species are known from the "Miocene" of southwest Honshu around the eastern part of the Seto Inland Sea.

*M. maximus* occurs from the Funazuan to the Nishisonogian Stages (Mizuno, 1962) of southwest Japan (e.g. Nagao, 1928b; Oyama *et al.*, 1960; Mizuno, 1964; Okamoto and Imamura, 1964; Okamoto, 1970; Shuto and Shiraishi, 1971; Kamada, 1980; Fuse and Kotaka, 1986; Shuto, 1991). Although the precise age of the stratotype of the Funazuan Stage, the Funazu Sandstone Member of the Iojima Formation in the Takashima Coalfield, west Kyushu, is unknown, a calcareous nannofossil biostratigraphy of the correlate Matsushima Group in the Sakito-Matsushima Coalfield (SK-MT in Figure 4) was studied by Okada (1992). Okada (1992) assigned this group to the Subzone CP 15b to CP 16a of Okada and Bukry (1980). In addition, Okada (1992) also correlated the Oniike Formation of the Sakasegawa Group in the Amakusa Coalfield (AM in Figure 4) and the Yotsuyama Formation of the Manda Group in the Miike Coalfield (MK in Figure 4), both of which are referred to the Okinoshiman Stage below the Funazuan Stage (Mizuno, 1964), to CP 14b to CP 15b. These calcareous nannofossil biostratigraphic data suggest that the lower limit of the Funazuan Stage is in CP 15b. According to Berggren *et al.* (1995), this calcareous nannofossil zone ranges from 36.0 to 34.3 Ma or the late Eocene. Okada (1992) also studied the age of the Nishisonogi Group in the Sakito-Matsushima Coalfield

(SK-MT in Figure 4), the stratotype of the Nishisonogian Stage by means of calcareous nannofossil biostratigraphy, and assigned the age of the upper part of the Nishisonogi Group to sometime during CP 17 to CP 19 on the basis of the occurrence of *Dictyococcites bisectus*. According to Berggren *et al.* (1995), the last occurrence of this species (cited as *Reticulofenestra bisecta* in Berggren *et al.*, 1995) is 23.9 Ma or the latest Oligocene. Concerning the Ashiya Group in the Chikuho Coalfield (CH in Figure 4), one of the correlatives of the Nishisonogian Stage, biostratigraphic studies were carried out by Saito and Okada (1984), Tsuchi *et al.* (1987), Okada (1992) and Ibaraki (1994). According to them, the age of the Ashiya Group is the late early to early late Oligocene. Further, the Taoyama Formation of the Hioki Group in the Yuyawan area (YY in Figure 4), another correlative of the Nishisonogian Stage, contains *D. bisectus* (Fuse and Kotaka, 1986). Ozaki (1999) also reported fission-track ages of  $25.2 \pm 1.7$  Ma and  $23.1 \pm 1.6$  Ma (error:  $1\sigma$ ) from the Hitomaru Formation which overlies the Taoyama Formation in the Yuyawan area. Taking these data into account, the range of *M. maximus* is regarded as late Eocene to Oligocene (Figure 4).

*I. (H.) hataii* is a species originally described from the "Miocene" Teshima Formation of the Tonosho Group in Teshima Island, northern Kagawa Prefecture (SH-TS in Figure 4; Noda and Furuichi, 1972). Bando and Furuichi (1978) correlated this formation to the Shikai Formation of the Tonosho Group in Shodoshima Island, situated several kilometers east of Teshima Island. This correlation is strongly supported by the occurrence of an endemic bivalve, *Tapes nagahamaensis* Saito, Bando and Noda, 1970, recorded only from the Teshima and Shikai Formations. Saito *et al.* (1970), Noda and Furuichi (1972), Bando and Furuichi (1978), Itoigawa and Shibata (1992) and Okumura and Sato (1999) all regarded the Tonosho Group distributed in Shodoshima and Teshima Islands as of early middle Miocene age. However, Kurita *et al.* (2000) reported the Eocene dinoflagellate cysts from the Shikai Formation. Consequently, the age of the Teshima Formation, which contains *I. (H.) hataii*, is also considered to be Eocene (Figure 4).

*C. (L.) namigataensis* was originally described from the "Miocene" Namigata Formation in Ibara City, Okayama Prefecture (NM in Figure 4; Ozaki, 1956). The age of the Namigata Formation has been considered to be the lowest middle Miocene (e.g. Shibata and Itoigawa, 1980; Itoigawa, 1983; Yano *et al.*, 1995a, b). Yano *et al.* (1995b) discriminated four benthic foraminiferal assemblages characterized by such species as *Elphidiella momiyamaensis* Uchio, *Pseudononion japonicum* Asano, *Hanzawaia tagaensis* Asano and *Cibicidoides pseudoungerianus* (Cushman) from the Namigata Formation. They pointed out that these assemblages are comparable with



**Figure 4.** Correlation of the selected Paleogene strata in Japan and chronologic range of molluscan species discussed in the text. Time scale: 1) Berggren *et al.* (1995); 2) Cande and Kent (1995) and Berggren *et al.* (1995); 3) Blow (1969); 4) Okada and Bukry (1980); 5) Mizuno (1962, 1964). e.: early; MAG.: Magnetic polarity; MIO.: Miocene; N.: Calcareous nannofossils; PL.: Planktonic foraminifera. AM: Amakusa Coalfield (Okada, 1992); AW: Awajishima area (Yamamoto *et al.*, 2000b); CH: Chikuhō Coalfield (Saito and Okada, 1984; Tsuchi *et al.*, 1987; Okada, 1992; Ibaraki, 1994); JB: Joban Coalfield (Tomida, 1986; Yanagisawa and Suzuki, 1987); KR: Karatsu Coalfield (Sakai *et al.*, 1990; Miyachi and Sakai, 1991; Okada, 1992; Ibaraki, 1994); MK: Miike Coalfield (Okada, 1992); NM: Nanigata area (Nishimoto and Itoigawa, 1977; SH-TS: Shidoshima-Teshima area (Kurita *et al.*, 2000); SK-MT: Sakito-Matsushima Coalfield (Okada, 1992); YY: Yuyawan area (Fuse and Kotaka, 1986; Ozaki, 1999). Mt.Gr.: Matsushima Group; Ns.Gr.: Nishisonogi Group; Sm.Gr.: Shimoshima Group.



those of the *Miogypsina kotoi*-*Operculina complanata* Assemblage Zone of Nomura (1992), being assigned to the latest early to early Middle Miocene. However, *E. momiyamaensis*, *H. tagaensis* and *C. pseudoungerianus* were also reported from the Iwaya Formation of the Kobe Group by Tai (1959), from which Yamamoto *et al.* (2000b) reported Eocene calcareous nannofossils and dinoflagellate cysts. In addition, the benthic foraminiferal assemblages from the Namigata Formation do not include *Ammonia tochiensis* (Uchio) which is one of the representative species in the Miocene benthic foraminiferal zone (Yano *et al.*, 1995b). Consequently, the benthic foraminiferal data do not indicate a Miocene age for the Namigata Formation.

On the other hand, Nishimoto and Itoigawa (1977) preliminarily reported *Carcharodon angustidens* (Agassiz) from the Namigata Formation in addition to the upper lower Oligocene Yamaga Formation of the Ashiya Group and the upper Oligocene Taoyama Formation of the Hioki Group. This fossil shark has very characteristic teeth with distinct anterior and posterior cusps. Yabumoto and Uyeno (1994) indicated that in Japan *C. angustidens* has been restrictedly found from the middle Eocene to the upper Oligocene of southwest Japan. Consequently, the age of the Namigata Formation is regarded to be somewhere during the middle Eocene to the late Oligocene, not the Miocene (Figure 4).

Although *C. (L.) namigataensis* was also recorded from the middle Miocene Kawazu Formation in Shimane Prefecture by Masuda (1962), his figured specimen (Masuda, 1962, pl. 21, fig. 1) is not referred to *Pecten* (*Chlamys*) *namigataensis* Ozaki, 1956 (see systematic paleontology to be discussed below). Recently, *C. (L.) namigataensis* was for the first time found from the Paleogene Iwaki Formation of the Shiramizu Group in the Joban Coalfield (JB in Figure 4), northeast Honshu, Japan. Nemoto and O'Hara (2001) figured a right valve of *Chlamys ashियाensis* (Nagao) from this formation, but their figured specimen is, in my opinion, *C. (L.) namigataensis* (see systematic paleontology). The age of the Iwaki Formation of the Shiramizu Group is considered to be the late Eocene or the early Oligocene on the basis of the occurrence of *Entelodon cf. orientalis* Dashzeveg (Tomida, 1986) and the planktonic microfossils age of the Shirasaka Formation (early Oligocene; Yanagisawa and Suzuki, 1987), the uppermost constituents of the Shiramizu Group.

Taking these facts into account, the geologic age of the Maéjima Formation is judged to be Paleogene, somewhere between the middle Eocene and late Oligocene.

#### Implications of the molluscan fauna of Maéjima Formation

Itoigawa (1983) grouped the "Miocene" molluscan as-

semblages from the First Setouchi Series in the coastal area of the eastern part of the Seto Inland Sea, including the Maéjima Formation, into four types, the *Cyclina-Barbatia*, the "*Ostrea*", the *Mactra-Acila* and the *Cyclocardia-Nuculana* assemblages. Constituents of these assemblages were considered to have inhabit the intertidal to uppermost sublittoral sandy mudbottom, uppermost to upper sublittoral rocky bottom, upper sublittoral sandy bottom, and upper sublittoral muddy bottom, respectively (Itoigawa, 1983). An assemblage comparable in generic composition to the *Mactra-Acila* assemblage was also recognized in the Maéjima Formation, namely, the *Megan-gulus-Acila* assemblage. Recent studies on planktonic microfossils (Kurita *et al.*, 2000, 2001; Yamamoto *et al.*, 2000b) indicate that some of the formations yielding these assemblages are of Eocene age, which concords with the results of the present study for age assignment.

It has been known that the four assemblages of Itoigawa (1983) have little similarity in not only specific but also generic compositions to the Miocene molluscan assemblages from the neighboring backbone area (e.g. Huzita, 1962; Itoigawa, 1969, 1971, 1983; Ueda, 1991; Yano *et al.*, 1995a). The latter assemblages are represented by the embaymental arcid-potamid [potamidid] fauna of Tsuda (1965). Yamamoto *et al.* (2000b) preliminarily considered that the difference between the assemblages from the coastal area of the Seto Inland Sea and those from the backbone area is chronological taking account of the Eocene planktonic microfossils from the Iwaya Formation of the Kobe Group, while previous researchers explained it by paleoenvironmental or paleogeographic factors in Miocene time (e.g. Itoigawa, 1983; Ueda, 1991; Takayasu *et al.*, 1992; Yano *et al.*, 1995a). The result of the present study supports the view of Yamamoto *et al.* (2000b), and both indicate that the Miocene First Seto Inland Sea (Ikebe, 1957) was not invaded in the coastal area of today's eastern part of the Seto Inland Sea, and that the "Miocene" shallow marine area in the eastern part of the Seto Inland Sea in the judgment of previous researchers (e.g. Shibata and Itoigawa, 1980; Itoigawa and Shibata, 1992; Takayasu *et al.*, 1992) was in fact of Paleogene age. Consequently, it is necessary to revise the Tertiary paleogeography of southwest Japan on the basis of the precise geochronologic data in near future.

It is notable that the molluscan fauna of the Paleogene Maéjima Formation contains both Tethyan Indo-Pacific elements and Northern Pacific elements of Honda (1991, 1994). The former are represented by such genera as *Isognomon* and *Septifer*, and the latter by, for example, *Cyclocardia* and *Megangulus* (Honda, 1994; Ogasawara, 1996). Honda (1994) revealed the northward migration of the Tethyan Indo-Pacific elements in the middle Eocene and the southward migration of the Northern Pacific ele-

ments during the late early Oligocene to early Miocene. However, the precise timing and mode of migration of the molluscan fauna have not fully been clarified because Paleogene shallow marine sediments were accepted to be almost lacking in the area between Kyushu and the Pacific coast of northeast Honshu. Although the precise geologic age of the Maéjima Formation was not determined by the molluscan evidence in the present study, further geochronological studies of the Paleogene shallow marine sediments in the coastal area of the eastern part of the Seto Inland Sea and taxonomical studies of the molluscan fauna will provide a reliable basis for elucidation of the successive changes of the Paleogene molluscan fauna in the Northwest Pacific region.

### Concluding remarks

Until the middle of 1990s, Paleogene marine sediments in southwest Japan had been considered to be restricted mostly to the Southern Shimanto Belt (Taira *et al.*, 1980) in the back arc of the Japanese Islands, except for Kyushu. Honda (1991, 1994) discriminated the North Japan-Western Okhotsk, Central Japan and Taiwan-South Japan Provinces from north to south for the western Pacific Paleogene molluscan faunal provinces. The Central Japan Province, in particular, was proposed on the basis of fragmental molluscan records from the accretionary sediments deposited in the lower sublittoral zone or at greater depths. Consequently, the characteristics of the shallow marine molluscan faunas in this province have been less than clear. The result of the present study strongly supports the age estimation based on planktonic microfossils by Kurita *et al.* (2000, 2001) and Yamamoto *et al.* (2000b) that the constituent formations of the "Miocene" First Setouchi Series in the coastal area of the eastern part of the Seto Inland Sea are in fact Paleogene, not Miocene (Kurita *et al.*, 2000, 2001; Yamamoto *et al.*, 2000b).

### Systematic description of selected taxa

All the illustrated specimens are housed at the Museum of Nature and Human Activities, Hyogo (MNHAH). The following institutional abbreviations are also used in this paper: IGPS: Institute of Geology and Paleontology, Tohoku University, Sendai; NSMT: National Science Museum, Tokyo; UMUT: University Museum, the University of Tokyo.

Class Bivalvia  
Subclass Paleotaxodonta  
Order Nuculoida  
Superfamily Nuculoidea  
Family Nuculidae

Genus *Acila* H. & A. Adams, 1858  
Subgenus *Truncacila* Grant and Gale, 1931,  
ex Schenck MS

*Acila (Truncacila)* sp. cf. *A. (T.) nagaoi*  
Oyama and Mizuno, 1958

Figure 5.4

#### Compare.—

*Acila nagaoi* Mizuno (MS). Mizuno, 1956, pl. 2, fig. 1.  
[*nomen nudum*]

*Acila (Truncacila) nagaoi* Oyama and Mizuno, 1958, p. 7–8,  
pl. 1, figs. 14, 15.

*Material*.—MNHAH reg. no. D1-018895 (from MJ-5).

*Discussion*.—The specimens from the Maéjima Formation are comparable with *Acila (Truncacila) nagaoi* Oyama and Mizuno, 1958, in having a small, rather longer than high, posteriorly oblique, oval shell with a beak situated at four-fifths of the shell length from the anterior end and a weak posterior ridge. They are not sufficiently well preserved to allow a precise species assignment.

Subclass Pteriomorphia  
Order Arcoida  
Superfamily Arcoidea  
Family Arcidae  
Subfamily Arcinae  
Genus *Arca* Linnaeus, 1758  
Subgenus *Arca* Linnaeus, 1758

*Arca (Arca) uedai* sp. nov.

Figure 5.5, 5.7a-c, 5.12

*Type specimens*.—MNHAH reg. nos. D1-018896 (Holotype); D1-018897 through D1-018903 (Paratypes).

*Type locality*.—Loc. MJ-4. A small outcrop exposure on its northern side about 400m south-southeast of Yoshida Shrine, Maéjima Island, Ushimado Town, Oku County, Okayama Prefecture (34° 36' 2" N, 134° 10' 29" E).

*Diagnosis*.—Rather small-sized *Arca (Arca)* with a low umbonal area, low crescent-shaped ligamental area, narrow hinge plate and shell surface sculptured by fine, low, numerous radial ribs.

*Description*.—Shell rather small (less than 40 mm in shell length), transversely elongate quadrate, inequilateral, moderately inflated; hinge line straight, long; beak blunt, prosocline, situated about two-fifths anteriorly of shell length; posterior ridge distinct, shell strongly depressed behind it; posteroventral margin obliquely truncated; central part of shell weakly depressed; shell surface sculptured by about 60 fine, low radial ribs; ribs generally with a fine intercalary rib on interspace; growth lines fine, generally



Table 2. Measurements of *Arca* (*Arca*) *uedai* sp. nov.

MNHA reg. no.	Length (mm)	Height (mm)
D1-018896*	34.2	18.8
D1-018897**	24.5***	12.3***
D1-018898**	35.0+***	15.2***
D1-018899**	30.9+	15.9

\*holotype. \*\*paratype. \*\*\*deformed

weak but rather strengthen on central depressed area; ligamental area low crescentic in shape, smooth except for one or a few, rather deep, chevron-shaped ligamental grooves; adductor muscle scars moderate in size, ovate (type A of Noda, 1966), weakly impressed; pallial line shallow, weakly impressed; inner ventral margin not crenated.

**Etymology.**—The present new species is named in honor of the late Tetsuro Ueda of Niigata University, who contributed to the molluscan paleontology of the First Setouchi Series during the middle 1980s to early 1990s.

**Discussion.**—*Arca* (*Arca*) *uedai* sp. nov. closely resembles *A. (A.) miurensis* Noda, 1966, from the Pleistocene Koshiba Formation in Kanagawa Prefecture. However, the present new species possesses a narrower hinge plate and lower ligamental area.

*A. (A.) sakamizuensis* Hatai and Nisiyama, 1952, from the Oligocene Sakamizu Formation of the Ashiya Group in Fukuoka Prefecture, Kyushu, is similar to the present new species in having fine radial ribs. The former is discriminated from the latter by having a more produced umbonal area and a higher ligamental area.

*A. (A.) washingtoniana* Dickerson, 1917, from the Oligocene Gries Ranch Formation of Washington, U.S.A., is another allied species, but is distinguished from *Arca* (*Arca*) *uedai* sp. nov. by having coarser radial ribs on the younger shell and stronger teeth.

The Recent *A. (A.) boucardi* Jousseaume is easily distinguished by having a larger shell with a stronger posterior ridge, coarser, less numerous radial ribs, and a higher umbonal area.

**Measurements.**—Table 2.

Order Mytiloida  
Superfamily Mytiloidea  
Family Mytilidae  
Genus *Septifer* Récluz, 1848  
Subgenus *Mytilisepta* Habe, 1951

*Septifer* (*Mytilisepta*) sp. indet.

Figure 5.8, 5.9, 5.14

**Material.**—MNHAH reg. nos. D1-18905 through D1-018907 (from MJ-2b), D1-018908 and D1-018909 (from

MJ-2c), D1-018910 (from MJ-4), and D1-018911 (from MJ-6).

**Discussion.**—Several poor specimens have been obtained. The occurrence of a septum in the subumbonal region and inner ventral margin lacking fine crenations indicate this species is referred to the subgenus *Mytilisepta* Habe, 1951.

*Septifer* (*Mytilisepta*) sp. from the Maéjima Formation is similar in general shell shape to *Septifer* (*Septifer*) *nagaoi* Oyama, 1951, which was introduced as a new name for *Mytilus hirsutus* Lamarck of Yokoyama, 1927 from the Oligocene Nishisonogi Group in Nagasaki Prefecture. However, the holotype designated by Oyama (1951) (UMUT reg. no. CM24987) has a very finely crenated inner ventral margin, as Mizuno (1952) described.

The present species is easily distinguished from the Recent species, *Septifer* (*Mytilisepta*) *keenae* Nomura, 1936 distributed in southern Hokkaido and southward, in having a larger shell with finer radial ribs and weakly curved anteroventral margin.

Order Pterioida  
Superfamily Pterioidea  
Family Isognomonidae  
Genus *Isognomon* [Lightfoot, 1786]  
Subgenus *Hippochaeta* Philippi, 1844

*Isognomon* (*Hippochaeta*) *hataii*  
Noda and Furuichi, 1972

Figures 5.15-5.17, 6.13, 6.14

*Isognomon* (*Isognomon*) *hataii* Noda and Furuichi, 1972, p. 120, text-fig. 1.

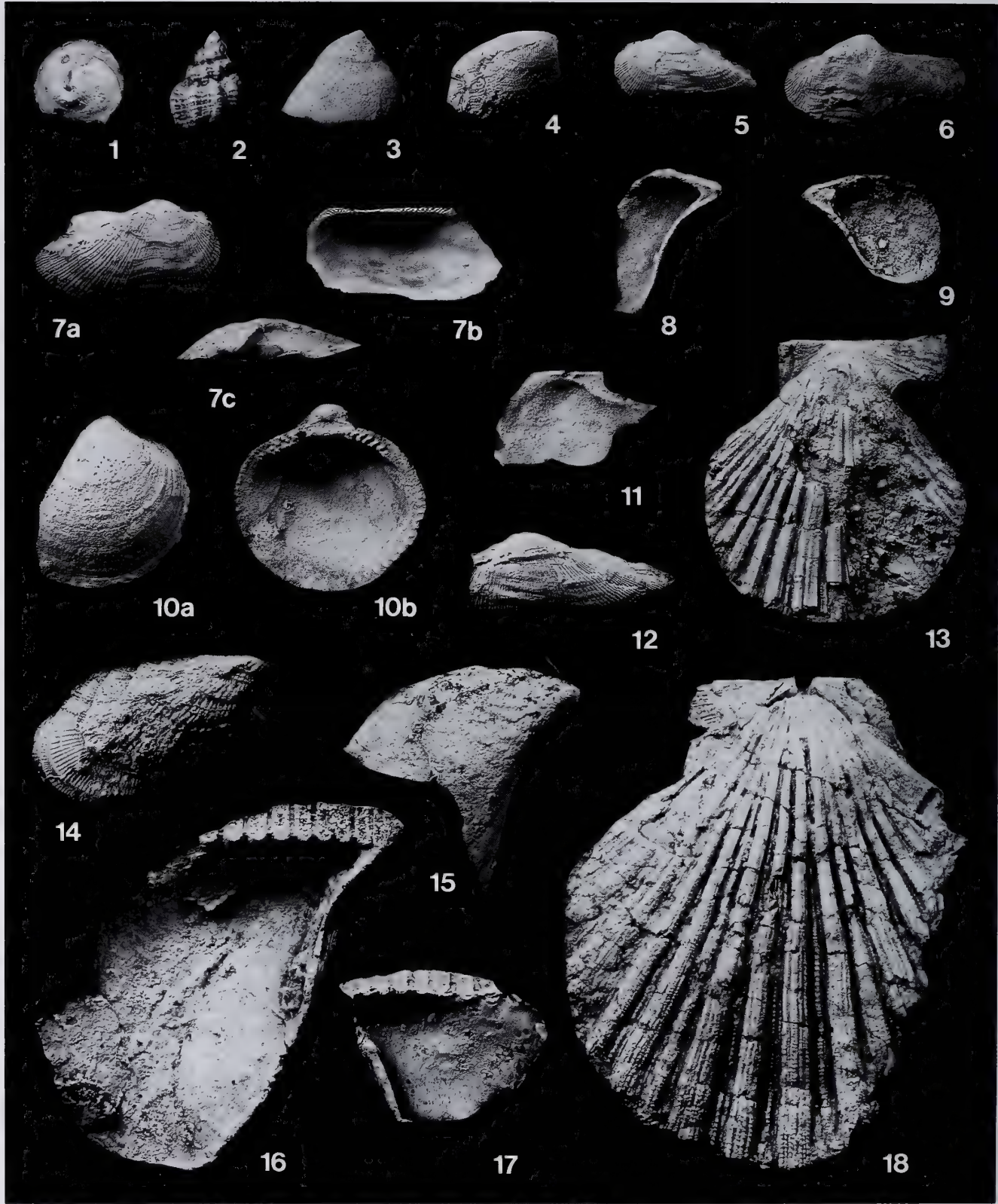
*Isognomon* (*Isognomon*) *hataii* Noda and Furuichi. Kaikiri and Nishimoto, 1995, p. 204.

**Type specimen.**—IGPS coll. cat. no. 91766 (Holotype).

**Material.**—MNHAH reg. nos. D1-018912 through D1-018918 (from MJ-1), D1-018919 through D1-018924 (from MJ-2a), D1-018925 through D1-018941 (from MJ-3), and D1-018942 (from MJ-6).

**Emended diagnosis.**—Shell of large size, mytiliform, rather thin except for ligamental area, moderately inflated; shell surface nearly smooth except for very fine, irregular, dense growth lines; byssal sinus roundly depressed; ligamental part rather thick; ligamental area rather broad, with 8 to 12 deeply concave resilifer grooves; lamellar ligament attachment area broader than groove, weakly depressed, surrounded by a fine ridge.

**Description.**—Shell rather large in size for the genus, mytiliform, rather thin except for ligamental area, moderately inflated; apical angle about 60°; byssal sinus rather depressed; posterodorsal margin nearly straight or weakly





curved; posteroventral margin nearly parallel to anterior one, weakly curved; centroventral margin arcuate and smoothly continuing to antero- and posteroventral margin; shell surface nearly smooth, sculptured only by very fine, irregular, dense growth lines; ligamental part thick; ligamental area rather broad, weakly annulated, with 8 to 12 resilifer grooves on fully grown individuals; resilifer grooves subequal, perpendicular to posterodorsal margin; lamellar ligament attachment areas weakly depressed, broader than resilifer grooves, surrounded by a fine ridge, with U-shaped inner margin; three byssal-pedal retractor muscle scars on subligamental part of internal shell; pallial line shallow, coarse, irregularly dotted near beak; adductor muscle scar indistinct.

**Discussion.**—The broad and shallow lamellar ligament attachment areas, narrow resilifer grooves and three byssal-pedal retractor muscle scars on the inner dorsal area indicate the Maéjima specimens are referred to the subgenus *Hippochaeta*. The ligamental area of the type species, *Perna maxillata* Lamarck, is well figured in Cox (1969) and Savazzi (1995).

The examined specimens from the Maéjima Formation can be referred to *Isognomon* (*Isognomon*) *hataii* Noda and Furuichi, 1972. This species was originally described from the Teshima Formation of the Tonosho Group in Teshima Island, Kagawa Prefecture, on the basis of a single incomplete left valve. Unfortunately, the shell features such as shape, thickness and surface sculpture are unknown because the holotype (IGPS coll. cat. no. 91766) is an internal mold lacking both shell material and the posterior half of the ventral area. Comparison with the holotype shows that apical angle and ligamental features are identical. Consequently, *I. (I.) hataii* is transferred here to the subgenus *Hippochaeta*, and the holotype is a fragmental juvenile specimen having less diagnostic characters.

Earlier Matsubara (2001) preliminarily identified *Isognomon* from the Maéjima Formation as *Pedalion murayamai* Yokoyama, 1932, originally described from the "Bed III" (= ? middle Eocene Krasnopoliievskaya Forma-

tion, after Kafanov and Amano, 1997) in the Dorogawa-Hishitori Region, south Sakhalin. However, it becomes clear that the Maéjima specimens have deeper resilifer grooves, less depressed lamellar ligament attachment areas, coarser pallial line, and a much more indistinct adductor muscle scar than *P. murayamai*. In addition, the byssal area of *P. murayamai* is rather distinctly bent, while that of the Maéjima specimens is gently curved. Consequently, the Maéjima specimens are not referred to this species. It may be noted that the holotype of *P. murayamai* (UMUT reg. no. CM27020) is missing.

The present species is also similar in shell shape to *Pedalion tomiyasui* Nagao, 1928a, from the middle Eocene Iojima Formation of the Okinoshima Group of Kyushu. However, it is easily distinguished from the latter species by having a larger shell with narrower resilifer grooves and weakly compressed lamellar ligament attachment areas.

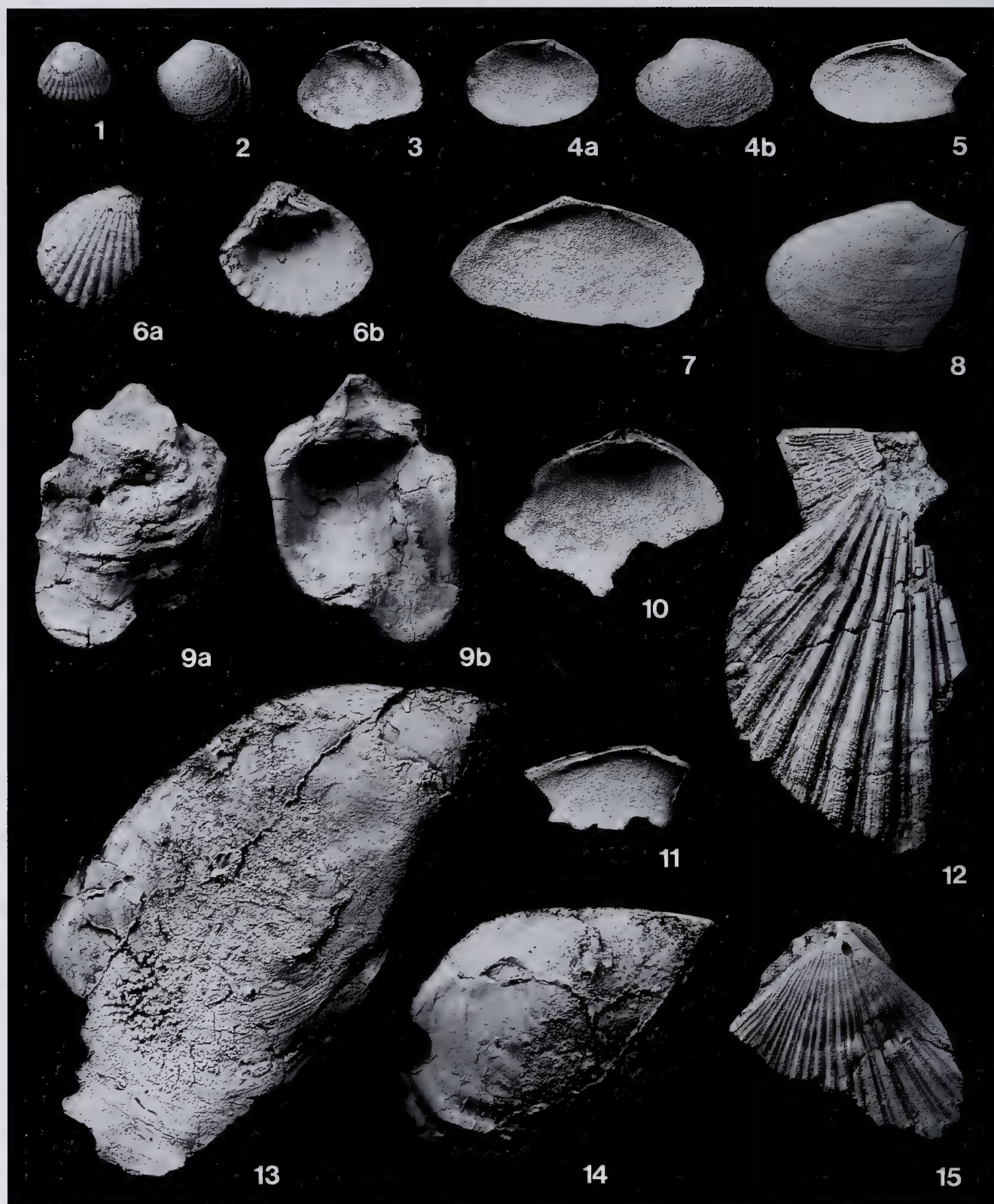
*Pedalion clarki* Effinger, 1938, originally described from the Oligocene Gries Ranch Formation of Washington, U.S.A., is another allied species, but differs in having more numerous resilifer grooves.

*Pedalion tugaruense* Nomura, 1935a, originally described from the lower middle Miocene Tanosawa Formation in Aomri Prefecture, northeast Japan, is easily distinguished from *I. (H.) hataii* by its thicker, much more longitudinally elongate shell with higher ligamental area and much blunter umbonal angle.

**Distribution.**—Teshima Formation of the Tonosho Group in Kagawa Prefecture, Eocene; Maéjima Formation in Okayama Prefecture, Eocene or Oligocene.

Order Ostreoida  
Superfamily Pectinoidea  
Family Pectinidae  
Subfamily Chlamydinae  
Tribe Chlamidini  
Genus *Chlamys* [Röding, 1798]  
Subgenus *Leochlamys* MacNeil, 1967

◀ **Figure 5.** Mollusca from the Maéjima Formation (1). All specimens in natural size, unless otherwise stated. All specimens whiten by magnesium oxide. 1. *Calyptraea* sp. Dorsal view of internal mold, MNHAH reg. no. D1-018890,  $\times 1.5$ . 2. Muricidae? gen. and sp. indet. Dorsal view, MNHAH reg. no. D1-018893, silicon rubber cast,  $\times 1.5$ . 3. Naticidae? gen. and sp. indet. Dorsal view, rather compressed, MNHAH reg. no. D1-018891, silicon rubber cast,  $\times 1.5$ . 4. *Acila* (*Truncacila*) cf. *nagaui* Oyama and Mizuno. Left valve, MNHAH reg. no. D1-018895, silicon rubber cast. 5, 6, 7a-c, 12. *Arca* (*Arca*) *uedai* sp. nov. 5. Left valve, MNHAH reg. no. D1-018897 (paratype). 6. Left valve, MNHAH reg. no. D1-018899,  $\times 1.5$ . 7a-c. Right valve, MNHAH reg. no. D1-018896 (holotype), silicon rubber cast. 7a. External view. 7b. Internal view. 7c. Umbonal view. 12. Left valve MNHAH reg. no. D1-018898 (paratype), compressed umbonal-ventrally. All specimens silicon rubber casts. 8, 9, 14. *Septifer* (*Mytilisepta*) sp. 8. Internal view of left valve, MNHAH reg. no. D1-018911. 9. Internal view of right valve, MNHAH reg. no. D1-018905. 14. Right valve, MNHAH reg. no. D1-018908. All specimens silicon rubber casts. 10a-b. *Glycymeris* (*Glycymeris*) sp. Left valve. MNHAH reg. no. D1-018904, silicon rubber cast. 10a. External view. 10b. Internal view showing especially strong teeth and ligamental area with chevron sculpture. 11. *Delectopecten* sp. Internal view of left valve, MNHAH reg. no. D1-018943, silicon rubber cast,  $\times 2$ . 13, 18. *Chlamys* (*Leochlamys*) *namigataensis* (Ozaki). 13. Right valve, MNHAH reg. no. D1-018945. 18. Left valve, MNHAH reg. no. D1-018944. 15, 16, 17. *Isognomon* (*Hippochaeta*) *hataii* Noda and Furuichi. 15. Right valve lacking ventral part. MNHAH reg. no. D1-018929. 16. Internal view of left valve. MNHAH reg. no. D1-018926. 17. Internal view of right valve, showing ligamental area. MNHAH reg. no. D1-018916. All specimens silicon rubber casts.





*Leochlamys* MacNeil, 1967, p. 9–10.

*Azumapecten* Habe, 1977, p. 82.

*Type species.*—*Chlamys* (*Leochlamys*) *tugidakensis* MacNeil, 1967, by original designation. Unnamed "Pliocene" in Tugidak Island, Alaska, U.S.A.

*Discussion.*—Habe (1977) proposed the subgenus *Azumapecten* on the basis of the following description: "Shell of small to moderate size; right valve rather inflated, with irregular, spiny radial ribs; left valve rather compressed; anterior and posterior auricles intercalating a beak between them, rather large; posterior auricle rather oblique; byssal notch on anterior part of right valve" (translated from Japanese by the present writer). *Pecten* (*Chlamys*) *farreri* Jones and Preston, 1904, living in the Northwest Pacific was designated as the type species.

The original description of *Azumapecten* involves several obscurities in the diagnosis and is not associated with any comparison to allied genera or subgenera. However, many malacologists have treated *Azumapecten* as a valid genus or subgenus (e.g. Habe, 1981; Waller, 1993; Hayami and Matsumoto, 1995; Wang, 1996; Higo *et al.*, 1999; Hayami, 2000).

On the other hand, MacNeil (1967) proposed the subgenus *Leochlamys* which was typified by *Chlamys* (*Leochlamys*) *tugidakensis* MacNeil, 1967. MacNeil (1967) and Sinelnikova (1975) also referred "*Chlamys nipponensis* Kuroda" (= *P. (C.) farreri*) to the subgenus *Leochlamys*. Indeed, the large anterior auricle, deep byssal notch, relatively strong ctenolium, irregular spiny radial ribs on shell surface, shagreen microsculpture at least on interspaces of ribs, and absence of distinct crenulations on the inner ventral margin are common to both subgenera. Consequently, *Azumapecten* Habe, 1977, is a junior synonym of *Leochlamys* MacNeil, 1967.

*Chlamys* (*Leochlamys*) *namigataensis* (Ozaki, 1956)

Figures 5.13, 5.18, 6.12, 6.15

*Pecten* (*Chlamys*) *namigataensis* Ozaki, 1956, p. 7–8, pl. 2, fig. 4.

*Chlamys* (*Mimachlamys*) *namigataensis* (Ozaki). Kaikiri and

Nishimoto, 1995, p. 204.

*Chlamys ashियाensis* (Nagao). Nemoto and O'Hara, 2001, pl. 2, fig. 2. [not of Nagao, 1928b]

not *Chlamys* (*Mimachlamys*) *namigataensis* (Ozaki). Masuda, 1962, p. 188, pl. 21, fig. 1. [*Chlamys* sp.]

*Type specimens.*—NSMT reg. no. P1–4379 (Holotype and paratypes). Although Ozaki (1956) noted a specimen registered under this number as the holotype, two unfigured specimens are also registered under the same number. They are paratypes.

*Material*—MNHAH reg. nos. D1–018944 through D1–018951 (from MJ-2c), and D1–018952 (from MJ-4).

*Emended diagnosis.*—Moderate-sized *Chlamys* (*Leochlamys*) with 15 to 19 highly elevated radial ribs; fine radial threads appearing above ribs on ventral half of disc; left valve with an intercalary rib; radial sculptures densely imbricated; anterior auricle large, with a deep byssal notch and strong byssal fasciole on right valve; shell surface sculptured by a shagreen microsculpture.

*Description.*—Shell moderate in size, slightly higher than long, suborbicular, rather thin; apical angle between 85° and 95°; both valves with a shagreen microsculpture; lacking internal rib carinae.

Right valve weakly inflated; radial ribs 18 to 19, rather irregular, highly elevated, with three radial striations making ridges; ribs on both dorsal parts finer than those on center, finely imbricated; interspace of ribs rather deep, with or without an intercalary rib; anterior auricle large, sculptured by 6 to 7 fine radial ribs; byssal notch deep; ctenolium several in number, strong; byssal fasciole broad, strongly annulated; posterior auricle about half the length of the anterior one, with 7 to 8 radial ribs, weakly oblique anteriorly; resilifer pit moderate in size, with a weak resilifer tooth on both dorsal flanks; anterior dorsal tooth weak, long.

Left valve also weakly inflated; radial ribs 15 to 18, highly elevated, rather regular, with three sharp primary striations; an intercalary rib on each interspace; postero-dorsal part sculptured by fine, imbricated, radial striations; secondary radial striations appearing at about 40 mm from

➡ **Figure 6.** Mollusca from the Maëjima Formation (2). All specimens natural size, unless otherwise stated. All specimens whitened by magnesium oxide. **1, 6a–b.** *Cyclocardia* sp. 1. Left valve, MNHAH reg. no. D1–018956,  $\times 2$ . 6a–b. Right valve. MNHAH reg. no. D1–018955. 6a. External view lacking umbonal and antero-ventral parts. 6b. Internal view, especially showing transported cardinal teeth, both of  $\times 1.5$ . Both specimens silicon rubber casts. **2.** Lucinidae gen. and sp. indet. Left valve, MNHAH reg. no. D1–018954, silicon rubber cast,  $\times 2$ . **3, 10.** *Macra?* sp. 3. Internal view of left valve, MNHAH reg. no. D1–018969, 10. Internal view of right valve, MNHAH reg. no. D1–018968. Both specimens silicon rubber casts,  $\times 2$ . **4a–b.** *Tapes?* sp. MNHAH reg. no. D1–018971,  $\times 2$ . 4a. Internal view. 4b. External view. Silicon rubber cast. **5, 7, 8, 11.** *Megangulus maximus* (Nagao). 5. Internal view of right valve, MNHAH reg. no. D1–018965,  $\times 2$ . 7. Internal view of left valve, MNHAH reg. no. D1–018964,  $\times 1.5$ . 8. Left valve lacking posterior part of shell, MNHAH reg. no. D1–018961,  $\times 1.5$ . 11. Internal view of right valve lacking ventral part, MNHAH reg. no. D1–018962,  $\times 2$ . All specimens silicon rubber casts. **9a–b.** *Crassostrea* sp. Left valve, MNHAH reg. no. D1–018953. 14a. External view. 14b. Internal view. **12, 15.** *Chlamys* (*Leochlamys*) *namigataensis* (Ozaki). 12. Left valve lacking posterior half of shell. MNHAH reg. no. D1–018946. 15. Left valve lacking ventral part and anterior auricle. MNHAH reg. no. D1–018947. **13, 14.** *Isognomon* (*Hippochaeta*) *hataii* Noda and Furuichi. 13. Right valve, slightly compressed, MNHAH reg. no. D1–018928. 14. Right valve, MNHAH reg. no. D1–018925. Both specimens silicon rubber casts.

beak; striations on radial ribs and internal ribs tending to become imbricated ventralward with growth; anterior auricle sculptured by 10 to 14 fine, imbricated radial ribs; posterior auricle as in right valve.

*Discussion.*—Masuda (1962) considered the present species to be a member of the subgenus *Mimachlamys* Iredale, 1929, as a result of examination of a single right valve collected from the middle Miocene Kawazu Formation in Shimane Prefecture. However, his specimen has lower radial ribs, a shallower byssal notch and a broader apical angle, and is not referred to the present species.

The specimens from the Maéjima Formation have a large anterior auricle, deep byssal notch with strong ctenolium, and distinct shagreen microsculpture. The shagreen microsculpture is one of the diagnostic features of the tribe Chlamidini (Waller, 1993). Thus, the present species is referred to the subgenus *Leochlamys* MacNeil, 1967. The diagnosis of the present species is emended as above, adding the right valve features.

Recently, Nemoto and O'Hara (2001) figured a right valve specimen identified as *Chlamys ashiyaensis* (Nagao, 1928b) from the upper Eocene or lower Oligocene Iwaki Formation of the Shiramizu Group in the Joban Coalfield, northeast Honshu, Japan. Their figured specimen (Nemoto and O'Hara, 2001, pl. 2, fig. 2) is, however, unmistakably referred to the present species. *Pecten* (*Chlamys*) *ashiyaensis* Nagao, 1928b is distinguished from *Chlamys* (*Leochlamys*) *namigataensis* (Ozaki) by having a more compressed shell with more numerous, lower, more irregular radial ribs lacking dense imbrications.

*Distribution.* — Namigata Formation in Okayama Prefecture, Paleogene; Iwaki Formation of the Shiramizu Group in Fukushima Prefecture, late Eocene or early Oligocene; Maéjima Formation in Okayama Prefecture, Eocene or Oligocene.

Subclass Heterodonta  
Order Veneroida  
Superfamily Carditoidea  
Family Carditidae  
Subfamily Venericardiinae  
Genus *Cyclocardia* Conrad, 1867

*Cyclocardia* sp. indet.

Figure 6.1, 6.6a–b

*Material*—MNHAH reg. nos. D1-018955 (from MJ-4), D1-018956 and D1-018957 (from MJ-5).

*Description.* — Shell small, ovate, longer than high, inequilateral, oblique anteriorly, weakly inflated; radial ribs 19 to 23, rather low, round-topped, less curved; radial ribs on anterior two-thirds of shell subequal to their interspaces and broader than them on posterior part; pallial line dis-

tinct; anterior adductor muscle scar ovate, distinct; posterior adductor muscle scar oblong, weakly impressed; inner ventral margin crenated.

*Discussion.* — A single articulated specimen and two right valves have been obtained. It is interesting that one specimen has a transposed hinge (Figure 6.6b).

*Cyclocardia* sp. from the Maéjima Formation closely resembles *Cyclocardia takedai* (Honda, 1980) (new name for *Venericardia elliptica* Takeda, 1953), from the middle to upper Eocene Poronai Formation of Hokkaido. However, the former species has round-topped radial ribs while those of the latter species are flat-topped.

*Cyclocardia tokunagai* (Yokoyama, 1924) from the lower Oligocene Asagai Formation in Fukushima Prefecture is another allied species. However, this species is distinguished from *Cyclocardia* sp. from the Maéjima Formation by having a more triangular, more inequilateral shell with longer posterodorsal margin, less curved ventral margin and more numerous radial ribs. The present species differs from *Cyclocardia siogamensis* (Nomura, 1935b), recorded from the lower-middle Miocene of Japan and Korea, in having a less inflated shell with lower and broader radial ribs.

Superfamily Tellinoidea  
Family Tellinidae  
Subfamily Tellininae  
Genus *Megangulus* Afshar, 1969

*Megangulus maximus* (Nagao, 1928) comb. nov.

Figure 6.5, 6.7, 6.8, 6.11

*Tellina maxima* Nagao, 1928b, p. 80, pl. 4, figs. 8–10.

*Angulus* (*Tellinides*) *maximus* (Nagao). Oyama *et al.*, 1960, p. 200–201, pl. 61, fig. 6; Kamada, 1980, p. 333, pl. Pg-18, fig. 7; p. 334, pl. Pg-19, figs. 15, 16; p. 335, pl. N-93, fig. 4; Fuse and Kotaka, 1986, pl. 18, figs. 20, 21.

? *Angulus* (*Tellinides*) *maxima* (Nagao). Matsumoto, 1964, p. 106, pl. 1, fig. 14.

*Type specimens.*—IGPS coll. cat. nos. 36412 (Holotype) and 36452 (Paratypes).

*Material.*—MNHAH reg. nos. D1-018960 (from MJ-4), D1-018961 through D1-018963 (from MJ-5), and D1-018964 through D1-018965 (from MJ-6).

*Description.* — Shell rather small, transversely elongate subelliptical, thin, slightly inequilateral, compressed; anterodorsal margin weakly curved; anterior dorsoventral margin rounded; posterodorsal margin nearly straight, narrowly depressed along ligament; posterior end oblique, narrow, subtruncated; beak low, pointed, weakly opisthocline, situated slightly posterior to middle of shell; posterior ridge weak; shell surface nearly smooth, sculptured by faint, very



fine, commarginal growth lines which are periodically strengthened; growth lines also rather strengthened on ventral part; hinge plate narrow; both valves with two small cardinal teeth and a weak, thin, long lateral tooth; posterior tooth of right valve and anterior tooth of left valve weakly bifid; nymph low; adductor muscle scars and pallial line indistinct.

**Discussion.**—Oyama *et al.* (1960) transferred the generic position of *Tellina maxima* Nagao, 1928b to *Angulus* (*Tellinides*) without discussion. Indeed, a thin, compressed shell with small cardinal teeth and weak posterior ridge of the present species could well be identical with those of the type species of *Tellinides*, *Tellina timorensis* Lamarck. However, the anterolateral tooth of the present species is much longer and less oblique than that of the latter. *Tellina nitidula* Dunker (= *Fabulina hokkaidoensis* Habe, 1961), the type species of *Nitidotellina* Scarlato, 1961, also resembles *T. maxima* in having a thin, compressed shell, but the anterior end of the anterolateral tooth on the right valve is angularly pointed ventralward (see Habe, 1977, pl. 41, fig. 5). The most appropriate genus for *T. maxima* is *Megangulus* Afshar, 1969. Although the members of this genus generally have a larger and thicker shell with surface sculptured by commarginal grooves, I assign *Tellina maxima* Nagao, 1928b to it on the basis of the cardinal properties (see Matsukuma *et al.*, 1988 for precise internal shell features of the Recent species).

*Megangulus maximus* (Nagao, 1928b) is closely similar to *Peronidia ochii* Kamada, 1962, originally described from the upper Eocene or lower Oligocene Iwaki and Asagai formations in Joban Coalfield, Fukushima Prefecture, northeast Japan. However, the former species presents a shorter shell with a more rounded posteroventral margin than the latter one.

*Angulus okumurai* Taguchi, 1992, from the lower Miocene Yoshino Formation in Okayama Prefecture, also resembles the present species. However, the former species is distinguished from it in having a larger, more equilateral shell with orthogyrous beak and more rounded posterior margin. The precise generic position of *A. okumurai* is also dubious because the cardinal properties have not been sufficiently examined.

*Tellina* (*Peronidea*) *lutea t-matsumotoi* Otuka, 1940, originally described from the Miocene "Wakkauenbetu Formation" of northern Hokkaido is distinguished from the present species in having a larger shell with a beak situated more anteriorly, and longer, more produced posterior dorsoventral margin.

*Tellina vestalioides* Yokoyama, 1920 is easily distinguished from the present species by having a more inflated shell with a stronger posterior ridge, weakly concave posteroventral margin behind a posterior ridge, more distinctly truncated posteroventral margin, and stronger cardi-

nal teeth.

Although Matsumoto (1964) reported *Angulus* (*Tellinides*) *maximus* (Nagao) from the lower Miocene Ôga Formation in Shizuoka Prefecture, his figured specimen has a more inflated shell with a beak situated slightly anterior to the middle of the shell, and is not referred to the present species. The specimen from the Ôga Formation of Matsumoto (1964) is probably conspecific with *Hiatula minoensis* (Yokoyama) sensu Shibata and Kato (1988).

**Distribution.**—Funazu Sandstone Member of the Iojima Formation of the Okinoshima Group in Nagasaki Prefecture, late Eocene; Kishima Formation in Saga Prefecture, latest late Eocene to earliest early Oligocene; Yamaga Formation of the Ashiya Group in Fukuoka Prefecture, latest early to early late Oligocene; Kiwado and Taoyama Formations of the Hioki Group in Yamaguchi Prefecture, late Oligocene; Maéjima Formation in Okayama Prefecture, Eocene or Oligocene.

#### Superfamily Mactroidea

#### Family Mactridae

#### Subfamily Mactrinae

#### Genus *Mactra* Linnaeus, 1767

#### *Mactra*? sp. indet.

Figure 6.3, 6.10

**Material.**—MNHAH reg. nos. D1-018967 (from MJ-4), and D1-018968 through D1-018970 (from MJ-6).

**Description.**—Shell rather small, roundly subtrigonal, slightly longer than high, moderately inflated; hinge plate narrow; cardinal and lateral teeth rather weak; anterior and posterior lateral teeth thin; resilifer small, shallowly depressed.

**Discussion.**—On the basis of cardinal properties, this species is unmistakably referred to the family Mactridae. Unfortunately, the presence or absence of a lamellar plate between resilifer and nymph, and the mode of pallial sinus were not examined in the present material due to poor preservation. Thus, the generic assignment is provisional.

"*Mactra* sp." was regarded as one of the characteristic elements of the *Mactra-Acila* assemblage from the "Miocene" around the eastern part of the Seto Inland Sea (Itoigawa, 1983).

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# Eocene shallow marine foraminifera from subsurface sections in the Yufutsu-Umaoi district, Hokkaido, Japan

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**Abstract.** In subsurface sections of the Yufutsu-Umaoi district, Hokkaido, northern Japan, three Eocene benthic foraminiferal assemblage zones were defined in the Ishikari Group and the overlying Poronai Formation. They are in ascending order: *Evolutinella subamakusaensis-Haplophragmoides crassiformis* Assemblage Zone, *Globocassidulina globosa-Criboelphidium sorachiense* Assemblage Zone, and *Bulimina schwageri-Angulogerina hannai* Assemblage Zone. Assemblages characterizing each zone indicate the littoral to the inner sublittoral, middle sublittoral, and outer sublittoral paleobathymetric zones, respectively. A foraminiferal fauna in the upper bathyal zone was also identified based on reinterpretation of previous studies. It is composed of calcareous species such as *Gyroidina yokoyamai* and *Plectofrondicularia packardii*. Abundant occurrences of agglutinated foraminifera in shallower paleoenvironment suggest brackish and related stratified-water paleoenvironments caused by freshwater input into an embayment called the “Poronai Sea”. Such stratified conditions in coastal shallow marine areas may have formed oxygen-depleted zones as suggested in the previous study. These data and their paleoenvironmental implications are expected to furnish a basis for further consideration on geohistory of the Paleogene formations and also on the Eocene foraminiferal fauna of the northwestern Pacific.

**Key words:** Eocene, foraminifera, Ishikari Group, paleoenvironment, Poronai Formation

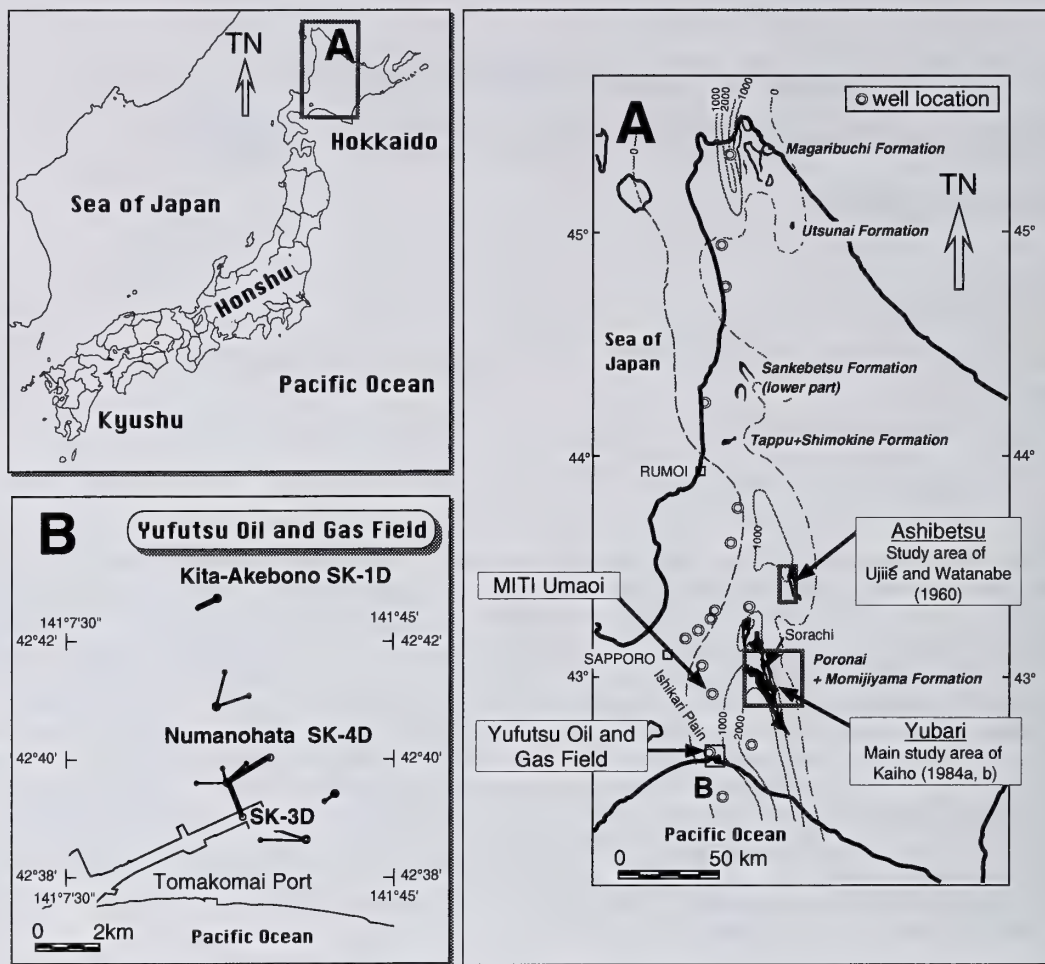
## Introduction

The purpose of the present paper is to delineate the Eocene shallow marine foraminiferal assemblages from borehole sections in the Yufutsu-Umaoi district, southern Ishikari Plain, Hokkaido, northern Japan; to consider depositional environments; and to describe paleobathymetric distributions of benthic foraminifera.

Studies of the Japanese Paleogene smaller foraminifera began with the report of Yokoyama (1890). Following him, studies have been conducted mainly on the fossils from the Ishikari Group and the overlying Poronai Formation in the coalfield regions of Hokkaido and from the Kyoragi Formation of the Hondo Group in the Amakusa Islands, Kyushu, southwestern Japan (e.g. Asano, 1952, 1954, 1958, 1962; Asano and Murata, 1957; Fukuta, 1962). Paleogene foraminiferal faunas at various localities in Hokkaido were studied by Kaiho (1983, 1984a, b, c) who reported on their stratigraphic and paleogeographic distributions. Kaiho (1992b) also conducted a com-

parative taxonomic study of the Paleogene foraminiferal faunas from Hokkaido with other regions of the world, and recognized some species from the Poronai Formation as an “intermediate-water” fauna. His “intermediate-water” has a depth range of 100–1000 m (Kaiho, 1992b). This range almost corresponds to three bathymetric zones in the modern northwestern Pacific coast of Japan according to the compilation of Akimoto and Hasegawa (1989). They are the outer sublittoral zone (approximately 70 to 180 m), upper bathyal zone (180 to 550 m) and upper middle bathyal zone (550 to 900 m). However, correlation of each paleobathymetric zone with the foraminiferal fauna was not discussed in the report.

Deep marine foraminiferal assemblages generally include elements transported from shallower marine environments by bottom currents and/or gravity currents (Zalesny, 1959; Ingle, 1980). This means that the deep marine fauna can be recognized only after the shallower marine fauna has been identified. However, little is known about the Paleogene shallow marine foraminiferal faunas in



**Figure 1.** Index map showing the well sections studied. A = Dashed lines denote isopachs of the Poronai Formation and its equivalents drawn in a 500-meter thickness interval (Japan Natural Gas Association and Japan Offshore Petroleum Development Association, 1992). Double circles indicate the sites of the wells controlling the isopachs. Dark areas show surface distribution of the Poronai Formation, Momijiyama Formation, and their equivalents after Yamada *et al.* (1982). B = Location of the wells in the Yufutsu oil and gas field. Double circles indicate the sites of the wells, and small dots indicate the bottom of the wells. Thick lines indicate wells used in this study.

Hokkaido. The material I examined in the present study is from marine strata (Poronai Formation) which grades from nonmarine coal-bearing formation (Ishikari Group), representing a transgressive phase, and thus provides an opportunity to study the shallow marine fauna. Moreover, because paleoenvironments of the Paleogene in Hokkaido and the northwestern Pacific region have not been well studied, data on paleobathymetric distribution of foraminifera examined in the present study are expected to provide a basis for further studies in the region.

Japan Petroleum Exploration Co. Ltd. (JAPEX) has been exploring oil and natural gas in the southern Ishikari Plain. Since the discovery of the Yufutsu oil and gas field, whose reservoir is in the Cretaceous granitoids and Paleogene conglomeratic formations, many wells have been drilled

penetrating the Paleogene rocks, namely, the Ishikari Group and the overlying Poronai Formation (Yufutsu Research Group of JAPEX Sapporo *et al.*, 1992; Fujii and Moritani, 1998; Kurita and Yokoi, 2000). The present study was conducted on three well sections in the Yufutsu oil and gas field, Numanohata SK-3D, Numanohata SK-4D and Kita-Akebono SK-1D. In addition, the well MITI Umai, drilled in the Umai Hills about 25 km north of the Yufutsu oil and gas field, was also investigated (Figure 1; MITI = Ministry of International Trade and Industry). The present study refers to the area including these wells as the "Yufutsu-Umai district".



### Geological setting

The middle Eocene Ishikari Group crops out in the hilly areas of the Yubari and Sorachi coal fields (Kaiho, 1983; Iijima, 1996). It is composed of alternating marine and nonmarine formations. Thick coal beds are present in the nonmarine part.

The Poronai Formation, which overlies the Ishikari Group, outcrops in the Yubari and Ashibetsu districts (Figure 1). It is composed mainly of massive siltstone that intercalates with acidic tuff beds in the middle to upper part (Kaiho, 1983). The geologic age of the Poronai Formation in the Yubari district was determined by calcareous nannofossils to be late Middle Eocene to Late Eocene in age (Okada and Kaiho, 1992). Broad distribution of the Poronai Formation and its equivalents in the subsurface of the Ishikari Plain is confirmed by boreholes (Figure 1A: Japan Natural Gas Association and Japan Offshore Petroleum Development Association, 1992; Japanese Association for Petroleum Technology, 1993).

Many researchers have discussed the stratigraphic relationship between the Ishikari Group and the overlying Poronai Formation since Yabe (1951) proposed their heteropic facies (synchronous) relationship (Asano, 1952, 1954; Saito, 1956; Sasa, 1956; Sasa *et al.*, 1953; Yabe and Asano, 1957; Uchio, 1961, 1962), although no conclusive interpretation has yet been drawn. The present study assumes a conformable contact between them in the borehole sections studied here. This interpretation is based on transitional characteristics of lithology as discussed later.

### Lithostratigraphy of study sections

Lithologic columns of the study wells are presented in Figure 2. Lithologic descriptions of each section are based on the wellsite survey of ditch cuttings. Numbers shown on the left of each column are drilling depths from the surface. All study wells of the Yufutsu oil and gas field are deviated, therefore drilling length differs from true thickness of formation. In addition, formation contacts are placed on the basis of wireline logs whose depths may not match the drilling depths measured by the length of drill pipes.

Interpretations of wireline logs prove that the uppermost part of the Poronai Formation is missing because of a fault in Numanohata SK-3D. Also because of a fault, an interval from the lowermost Poronai Formation through the upper part of the Ishikari Group is repeated in Numanohata SK-4D.

After correcting for well deviations and formation dips, the true thickness of the Poronai Formation in the Yufutsu oil and gas field is estimated as approximately 450 m to 500 m, while in the vertical well MITI Umaoi, it is approxi-

mately 780 m.

Lithology of the Ishikari Group and the Poronai Formation in the study well sections is similar. Its vertical changes are as follows in ascending order; basal conglomerate bed, medium to finer sandstones with siltstone beds, and finally siltstones and mudstones. The basal conglomerate of the lowermost part of the Ishikari Group grades upward, intercalating with finer-grained sediments, into an alternation sequence of medium to fine sandstone beds and olive-black to olive-gray siltstone beds. Coal beds are frequent. The sandstone and siltstone beds of the uppermost Ishikari Group grade upward into the siltstone and mudstone of the Poronai Formation, which contains marine fossils such as foraminifera, ostracods, dinoflagellates, and fragments of mollusks. The Poronai Formation consists mainly of olive-gray or dark gray siltstone and mudstone. Tuff and sandstone beds intercalate in the upper part of the formation in Kita-Akebono SK-1D and MITI Umaoi, where the formation is thicker than in the other well sections. The Upper Oligocene Minaminaganuma Formation unconformably overlies the Poronai Formation in the Yufutsu-Umaoi district (Kurita and Yokoi, 2000). The Lower Oligocene Momijiyama Formation (Kaiho, 1983; Kurita and Miwa, 1998), which overlies the Poronai Formation in the Yubari district, is not present in the study area.

The upward fining of the sediments without any break from the Ishikari Group to the lower part of the Poronai Formation in the Yufutsu-Umaoi district suggests a transgressive sequence.

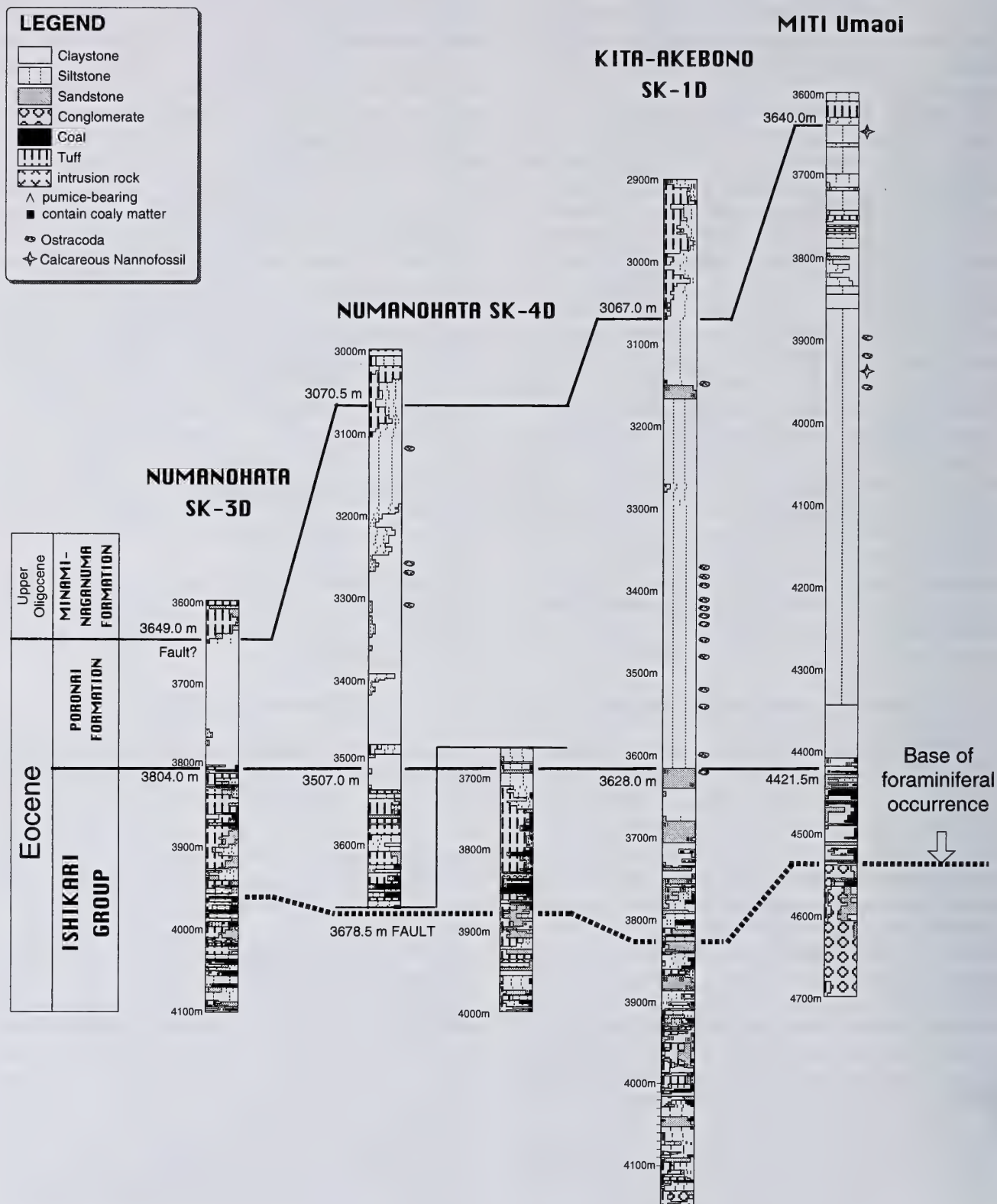
### Samples and methods

All borehole samples used in the present study are ditch cuttings. Borehole conditions during drilling were good, and contamination caused by the caving was negligible. Samples were taken every 20 m; additional samples were taken from the siltstones in the coal-bearing formation. In the Kita-Akebono SK-1D well, samples were collected at every 10 m for most of the studied interval. A total of 173 samples were examined.

All samples were oven-dried. Subsamples of about 100 g were soaked in boiled sodium sulfate supersaturated solution for about three hours. After removing excess solution, soaked samples were left more than three days. Then they were wet sieved through a 125  $\mu$ m-opening screen. All specimens in the residues were picked and identified under a binocular microscope.

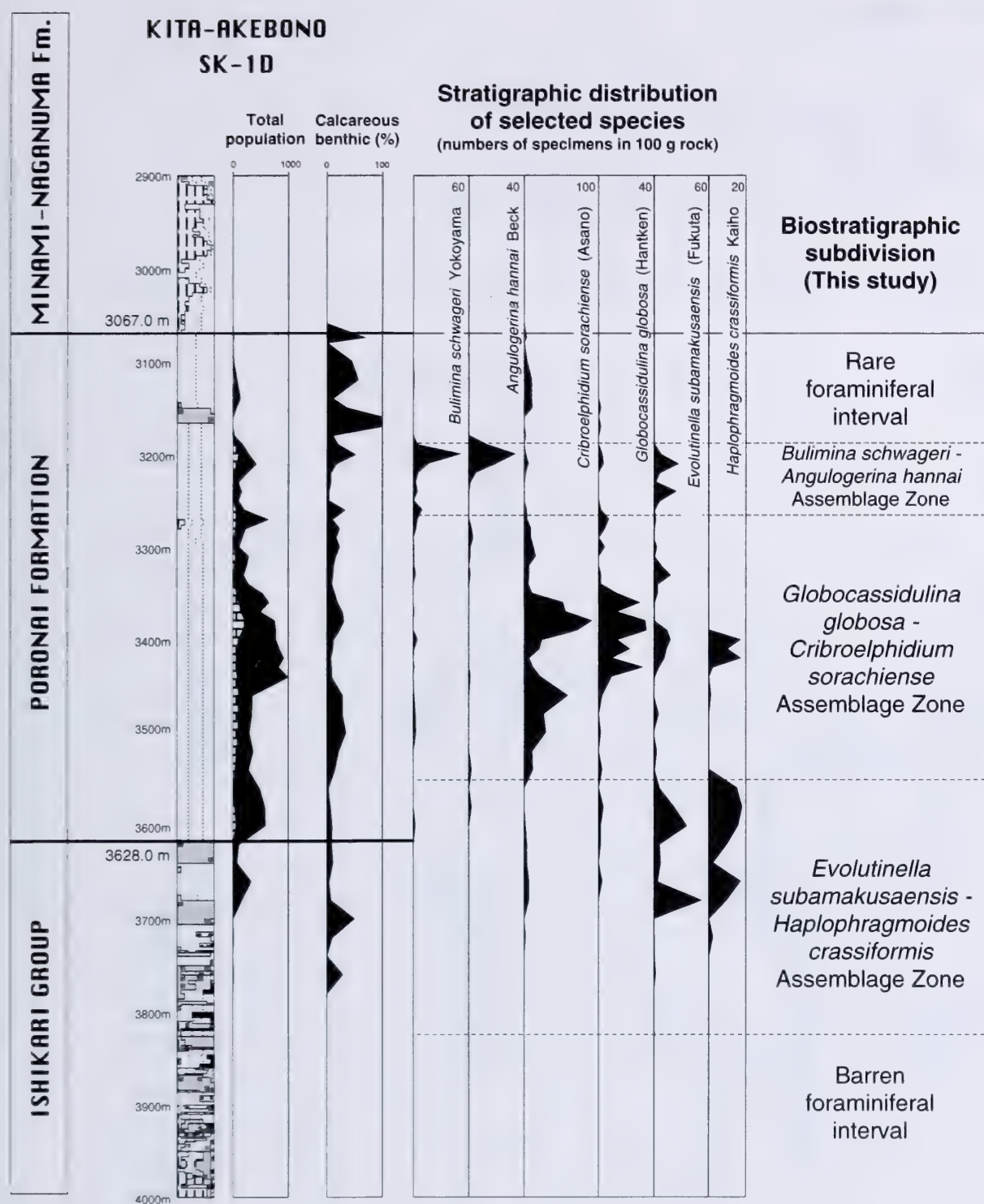
Percentages of planktonic species, agglutinated species, and calcareous benthic species, and total populations were determined for these samples. Diversity, species richness (number of species) as well as "Simpson's Index for Diversity" (SID: Simpson, 1949) were used to analyze the

# South



**Figure 2.** Stratigraphic correlation based on lithostratigraphy and wireline geophysical loggings of the study wells. Well sections are arranged at the base of the Poronai Formation.











For Legend, see Figure 2.

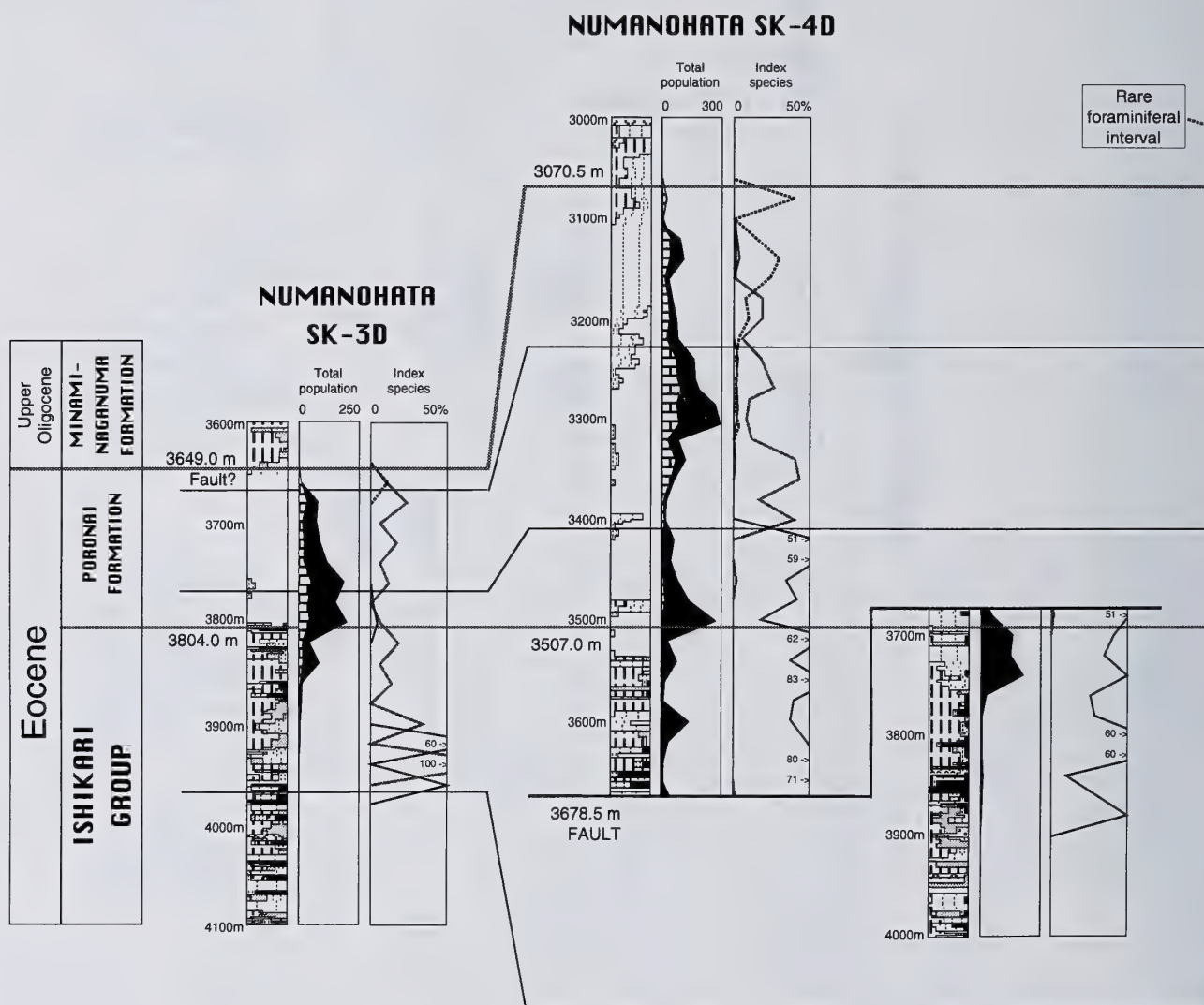
Figure 3. Stratigraphic occurrences of the selected species in Kita-Akebono SK-1D.

# South

## LEGEND

-  Total population of Calcareous Benthic foraminifera
-  Total population of Porcellaneous foraminifera
-  Total population of Agglutinated foraminifera
-  Percentage of *Evolutinella subamakusaensis* + *Haplophragmoides crassiformis*
-  Percentage of *Globocassidulina globosa* + *Cribroelphidium yabei*
-  Percentage of *Bulimina schwageri* + *Angulogerina hannai*

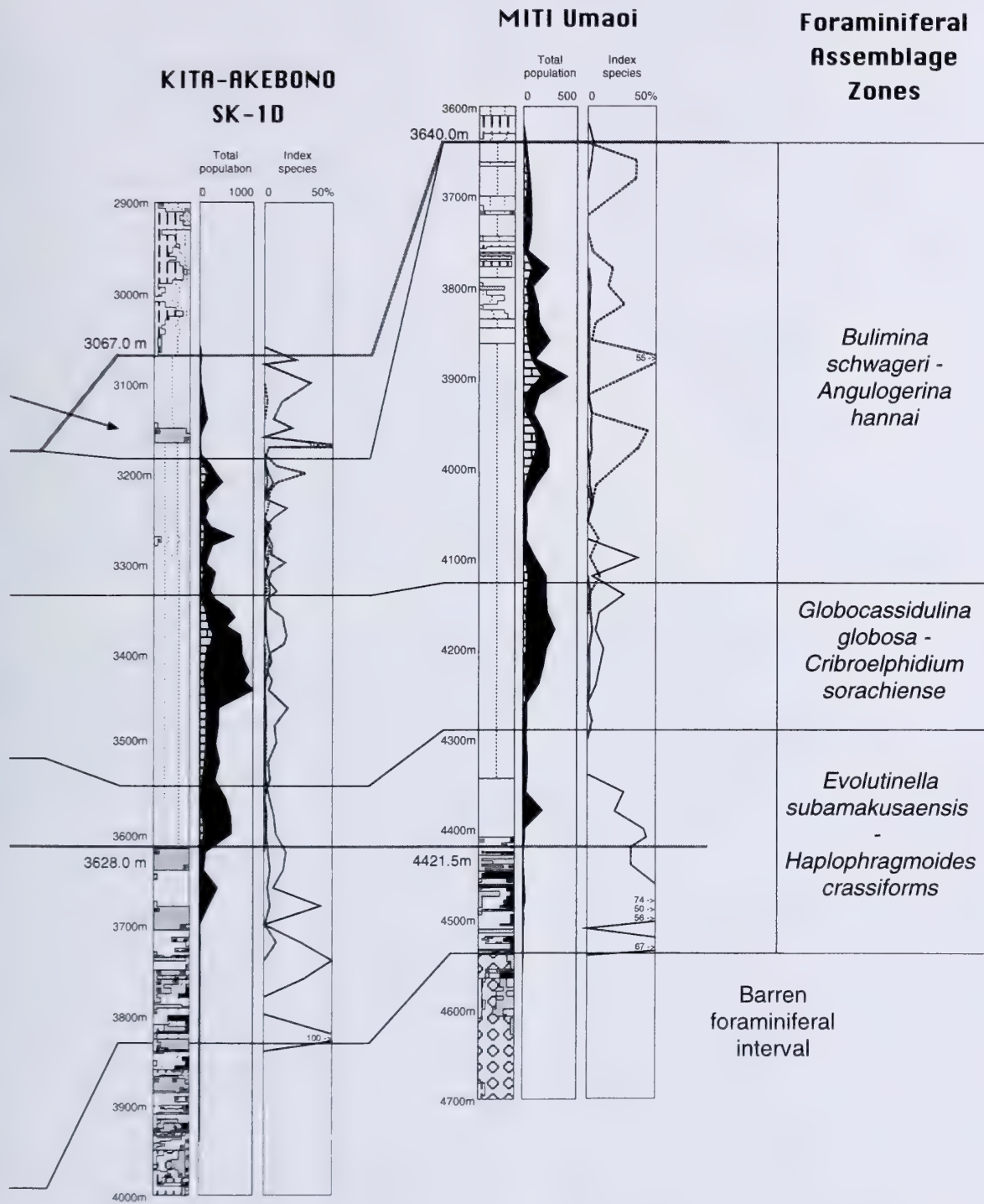
For lithology, see Figure 2.



**Figure 4.** Stratigraphic correlation of the study wells based on the assemblage zones of foraminifera. Left columns of each well section are cumulative (agglutinated, porcellaneous and calcareous foraminifera) total populations in 100 g rock samples. Curves in right column indicate percentage of index species against total population.



# North



assemblages.

Only populations of specimens identified at species rank were used to calculate diversity; species identified as "spp.", "sp. indet.", and "miscellaneous" were excluded.

### Biostratigraphy

As a result of analysis, 47 species belonging to 34 genera were identified from 162 samples (Appendix 1–3). Preservation of most specimens was poor.

The present study established assemblage zones based on associations of index species based on the foraminiferal distribution. Index species are species that are abundant and have similar stratigraphic distribution among all borehole sections.

Occurrences of selected species are plotted against depth for Kita-Akebono SK-1D (Figure 3). This plot reveals that some of the species have distinct similarities in stratigraphic occurrences. On the basis of this, the following three associations are recognized.

- 1) *Evolutinella subamakusaensis* and *Haplophragmoides crassiformis*.
- 2) *Globocassidulina globosa* and *Criboelphidium sorachiense*.
- 3) *Bulimina schwageri* and *Angulogerina hannai*.

These three associations represent zones which occur in all the studied sections in the same stratigraphic order, and each has a unique distribution within the section (Figure 4). The upper part of the Poronai Formation above the *Bulimina schwageri*-*Angulogerina hannai* Assemblage Zone in Kita-Akebono SK-1D (depth 3200–3075 m) is referred to here as "rare foraminiferal interval" because the number of foraminifera in the interval is so small. As discussed later, boundaries between these assemblage zones are environmentally controlled and therefore may not indicate strict time horizons.

Characteristics of each assemblage zone are discussed below. Boundaries between the zones are defined by changes in the abundances of the index species.

*Evolutinella subamakusaensis*-*Haplophragmoides crassiformis* Assemblage Zone.—This zone is characterized by abundant occurrences of the two index species. It also characteristically includes agglutinated foraminifera such as *Reticulophragmium amakusaensis*, *Cyclammina pacifica*, and *Recurvoidella* sp. cf. *R. lamella*. The calcareous foraminifer *Criboelphidium sorachiense* occurs rarely in this zone. Assemblages of this zone are characterized by generally small populations and low diversity.

*Globocassidulina globosa*-*Criboelphidium sorachiense* Assemblage Zone.—In addition to the two index species, this zone includes abundant agglutinated foraminifera such as *Evolutinella subamakusaensis*, *Recurvoidella* sp. cf. *R. lamella*, and *Budashevaella symmetrica*, and more calcare-

ous species such as *Melonis pompilioides* and *Pullenia salisburyi* than in the assemblages of the underlying *E. subamakusaensis*-*H. crassiformis* Assemblage Zone.

*Bulimina schwageri*-*Angulogerina hannai* Assemblage Zone.—Although this zone is similar to the *G. globosa*-*C. sorachiense* Assemblage Zone, it is distinguished by larger numbers and higher frequencies of both *Bulimina schwageri* and *Angulogerina hannai*. Assemblages of this zone also contain numerous agglutinated foraminifera, but have higher calcareous foraminiferal abundances and higher species diversities compared to those of the previous two assemblage zones.

### Paleoenvironment

The foraminiferal fauna seen in the present material is characterized by the occurrence of abundant agglutinated foraminifera, especially species belonging to the Lituolidae and Cyclamminidae. No similar fauna so dominated by these agglutinated foraminifera has been reported from anywhere else in the world. Therefore, paleoenvironmental implications of this peculiar fauna are considered based on the facts of modern foraminiferal distribution. In this section, the paleobathymetry of each assemblage zone and then the additional paleoenvironmental implications are discussed.

### Paleobathymetry

As discussed by Ingle (1980) and McDougall (1980), paleobathymetric zonations of the Eocene Pacific Ocean are similar to the modern zonations. Paleobathymetric zonations used in the present study follow Akimoto and Hasegawa (1989)'s compilation of bathymetric distributions of Recent benthic foraminifera around the Japanese Islands.

*Evolutinella subamakusaensis*-*Haplophragmoides crassiformis* Assemblage Zone.—This zone is considered to have been deposited in a shallow marine environment for the following reasons. First, it overlaps the coal-bearing formation of the Ishikari Group that is of paralic origin. Second, it yields benthic foraminifera *Criboelphidium sorachiense* and *Sigmoidella pacifica*, both of which suggest shallow marine (sublittoral) deposition. Most modern *Criboelphidium* live in shallow marine (outer sublittoral zone or shallower) environments, such as *Criboelphidium bartletti* (*Elphidium bartletti* of Loeblich and Tappan, 1953), *C. clavatum* (*E. clavatum* of Buzas, 1966 and Lagoe, 1979). *Sigmoidella pacifica* also lives in modern shallow marine environments (Jones, 1994, as *S. elegantissima*). Third, assemblages of this zone lack *Globocassidulina* and *Bulimina* whose modern species live at depths greater than the inner sublittoral zone in the seas around the Japanese Islands (Akimoto and Hasegawa, 1989). Thus, the assem-



blages of the *E. subamakusaensis* — *H. crassiformis* Assemblage Zone are considered to indicate a paleobathymetric range from the littoral zone to the inner sublittoral zone.

*Globocassidulina globosa*-*Criboelphidium sorachiense* Assemblage Zone. —The assemblages of this zone include *Globocassidulina*, which has its upper depth limit in the middle sublittoral zone (Akimoto and Hasegawa, 1989). In addition, *C. sorachiense*, *C. wakkanabense* and *Sigmoidella pacifica*, all of which indicate shallow marine environments, occur frequently in this zone. Therefore, the assemblages of the *G. globosa* — *C. sorachiense* Assemblage Zone are thought to indicate the middle sublittoral zone.

*Bulimina schwageri*-*Angulogerina hannai* Assemblage Zone. —The assemblages of this zone are similar to those of the *Globocassidulina globosa*-*Criboelphidium sorachiense* Assemblage Zone except that the percentages of *Bulimina* and *Angulogerina* are higher. Since modern species of *Bulimina* and *Angulogerina* have upper depth limits in the outer sublittoral (Akimoto and Hasegawa, 1989), the *Bulimina schwageri*-*Angulogerina hannai* zone is considered to have been deposited in the outer sublittoral zone. The presence of *Criboelphidium* species suggests either *in situ* deposition or transport of shallower-water species into the outer sublittoral zone, possibly by marine currents.

Kaiho (1992b) reported *B. schwageri* and *A. hannai* in his "intermediate-water" which ranges from depths of 100 to 1000 m. As the depth range of the outer sublittoral zone overlaps the range of Kaiho's "intermediate water," the present study agrees with Kaiho's interpretation on *B. schwageri* and *A. hannai*.

*Historical paleobathymetric change.* —Paleobathymetric interpretation of the three assemblage zones shows that the sedimentary environments during the deposition of the upper part of the Ishikari Group and the Poronai Formation in the Yufutsu-Umaoi district changed from the littoral zone to the inner sublittoral zone, then to the middle sublittoral zone, and finally to the outer sublittoral zone. The successive change in paleobathymetry suggests that the stratigraphic interval from the first occurrence of foraminifera to the *B. schwageri*-*A. hannai* Assemblage Zone was deposited during a single transgressive phase. This interpretation supports the observation that the Ishikari Group and the Poronai Formation are conformable in the Yufutsu-Umaoi district.

The "rare foraminiferal interval" at the depth 3190 m and shallower in Kita-Akebono SK-1D well indicates that a regressive phase followed the transgression discussed above. Evidence of the regression is based on the successive disappearances of the species, *B. schwageri*, *A. hannai*, *G. globosa*, and *C. sorachiense*. Shoaling of water depth prevented distribution of these depth-controlled species.

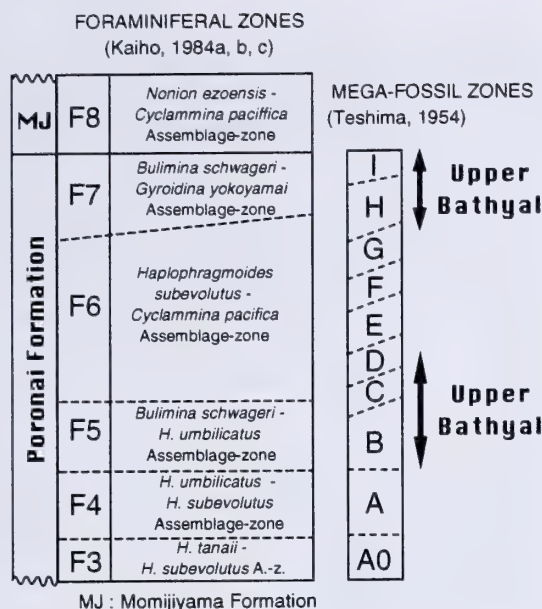


Figure 5. Stratigraphic relation between the megafossil zones and foraminiferal assemblage zones.

Consequently, the interval from the coal-bearing formation of the Ishikari Group to the Poronai Formation in the Yufutsu-Umaoi district accumulated during a single transgressive and regressive sequence. This is only observed in the Kita-Akebono SK-1D well, since the uppermost part of the Poronai Formation is missing in the other well sections.

### Upper bathyal assemblages

As a result of the study discussed above, species compositions from the littoral zone to the outer sublittoral zones during the Eocene were described. Foraminiferal fauna of the upper bathyal zone (water depth approximately 180 to 550 m in northwestern Pacific coast of northern Japan), which is one rank deeper than the outer sublittoral zone, is not observed in the Yufutsu-Umaoi district. However, existence of strata which show the upper bathyal environment was reported by Teshima (1955) in the middle part of the Poronai Formation in the Yubari district. Here, I describe upper bathyal foraminiferal fauna based on the correlation between biostratigraphy of Teshima (1955) and Kaiho (1984a, b). Teshima (1955) studied megafossils and divided the Poronai Formation into the A to I megafossil zones in ascending order, stating that the megafossil assemblages of the B-C and H-I zones are similar to the molluscan association found in water depth interval of 200 to 300 m, offshore Otaru, Sea of Japan. This water depth in the Sea of Japan falls within the range of the upper bathyal zone (Akimoto and Hasegawa, 1989). According to the stratigraphic relationship between these megafossil

Species		Sublittoral			Bathyal
		Inner	Middle	Outer	Upper
AGGLUTINATED					
Alveolophragmium	sp. A of the present study		R		
Ammobaculites	sp. A of Kaiho, 1984b			A	
Ammobaculites	akabiraensis Asano	R	R	R	
Ammodiscus	parianus Hedberg		R	C	R
Ammodiscus	tenuis Brady		R	C	C
Ammomarginulina	sp. A of Kaiho, 1984b			R	
Bathysiphon	eocenica Cushman and Hanna	R	R	C	C
Bathysiphon	vernoni Hamlin	R	R	R	C
Budashevaella	sp. aff. B. multicamerata (Voloshinova)			R	
Budashevaella	symmetrica (Ujiié and Watanabe)	R	C	C	R
Cribrostomoides	sp. cf. C. cratacea Cushman and Goudkoff		R	R	?
Cyclammina	ezoensis Asano	R	R	R	R
Cyclammina	orbicularis Brady			R	
Cyclammina	pacifica Beck	R	C	A	A
Cyclammina	sp. aff. C. pusilla Brady	R	R	R	R
Cyclammina	tani Ishizaki				R
Cyclammina	sp. A of the present study		R		
Cyclammina	sp. B of the present study	R			
Discammina	sp. A of Kaiho, 1984b	R	R	C	R
Discammina	sp. B of Kaiho, 1984b		?	R	R
Discammina	sp. C of Kaiho, 1984b	R	R	R	
Eggerella	sp. A of Kaiho, 1984b			R	
Evolutinella	subamamusaensis (Fukuta)	A	C	R	R
Glomospira	gordialis Jones and Parker				
Glomospira	crassiformis Kaiho	C	C	R	R
Haplophragmoides	sp. cf. H. deflata Sullivan				R
Haplophragmoides	rugosus soyaensis Yasuda		C	C	R
Haplophragmoides	tanaii Kaiho		C	C	
Haplophragmoides	yokoyamai Kaiho		R	R	R
Haplophragmoides	sp. A of the present study			R	?
Haplophragmoides	sp. B of the present study	R	R	R	?
Haplophragmoides	sp. D of the present study	C	R	R	?
Hyperammina	elongata Brady			R	
Karreriella	sp. cf. K. hokkaidoana (Takayanagi)			C	R
Martinottiella	crassa Kaiho			R	
Martinottiella	rectidellata Kaiho				R
Placentammina	sp. A of the present study		R	R	?
Poronaiia	poronaiensis (Asano)	C	R	C	R
Recurvoidella	sp. cf. R. lamella (Grzybowski)	A	C	C	?
Recurvoides	sp. A of the present study			R	?
Reophax	minutirectus Kaiho				R
Reophax	multicameratus Kaiho			R	C
Reophax	tappuensis Asano	C	C	C	C
Reticulophragmium	amamusaensis (Fukuta)	C	C	A	?
Rhabdammina	sp.			R	R
Silicosigmolinella?	sp.				R
Spiroplectammina	nuttalli Lalicker				R
Trochammina	sp. cf. T. asagaiensis Asano		C	C	R
Trochammina	squamata Jones and Parker			C	R
Verneulinula	takayanagii (Kaiho)			R	R
PORCELLANEUS					
Quinqueloculina	seminula compacta Serova	R	C	C	R
Triloculina	gibba d'Orbigny	R	R	R	R
CALCAREOUS HYALINE					
Anomalinoidea	sasai Kaiho			R	C
Anomalinoidea	sp. A of Kaiho, 1984b				R
Bolivina	euplectella Yokoyama				R
Brizarina	saitoi Kaiho	R	C		C
Brizarina	serrata Kaiho				C
Bulimina	schwageri Yokoyama	A	A		A
Bulimina	sculptilis Cushman				C
Bulimina	sp. cf. B. sculptilis Cushman		R	C	C
Bulimina	yabei Asano and Murata		C	R	
Buliminella	robertsi Howe and Ellis		C		
Cancris	torquatus Cushman and Todd				R
Cassidulina	lobatula Kaiho				R
Cassidulina	yubariensis Kaiho		R		R
Cassidulinoides	howei Cushman				C
Chilostomella	sp. cf. C. cylindroides Reuss				R
Cibicides	elmaensis Rau		R	R	R
Cibicides	complanatus Kaiho			R	
Cibicides	sp. A of Kaiho, 1984b			R	
Cibicides	sp. B of Kaiho, 1984b				R
Sublittoral					
Bathyal					
Inner					
Middle					
Outer					
Upper					
Cribroelphidium	ishikariense (Kaiho)	R	R	R	R
Cribroelphidium	sorachiense (Asano)	R	A	A	C
Cribroelphidium	sorachiense (Asano) var. A				
Cribroelphidium	wakkanabense (Kaiho)	R	C	A	
Dentalina	sp. cf. D. kushiroensis Yoshida				
Dentalina	sp. cf. D. subsoluta (Cushman)				C
Dentalina	cocconeis (Cushman)			R	C
Dentalina	dusenburyi Beck			R	C
Dentalina	minuta Kaiho				R
Elphidium	mabutii Asano*	?	?	R	?
Elphidium	sp. A of Kaiho, 1984b				
Epistominella	exigua multiloculata Kaiho				C
Eponides	lobatus Kaiho			R	C
Fissurina	marginata (Montagu)		R	R	C
Fissurina	sp. A of Kaiho, 1984b			R	C
Fursenkoina	uchioi Kaiho			R	C
Glandulina	laevigata ovata Cushman and Applin		C	C	C
Globobulimina	ezoensis (Yokoyama)			C	C
Globocassidulina	globosa (Hantken)		A	C	C
Globocassidulina	sp. A of Kaiho, 1984b			R	C
Globulina	gibba (d'Orbigny)			R	C
Guttulina	problema (d'Orbigny)	C	C	C	C
Guttulina	takayanagii Kaiho	R	R	R	R
Gyroidina	yokoyamai (Ujiié and Watanabe)				A
Heterolepa	poronaiensis Kaiho	R	R	C	
Lagena	sp. cf. L. laevis (Montagu)	R	R	R	R
Lagena	sp. cf. L. perlucida (Montagu)				C
Lagena	sp. cf. L. sulcata (Walter and Jacob)			R	
Lagena	striata (d'Orbigny)				R
Lagena	sp. A of Kaiho, 1984b				R
Lenticulina	antipoda (Stache)				C
Lenticulina	ishikariensis Kaiho				C
Lenticulina	sp. A of Kaiho, 1984b			R	R
Lenticulina	sp. B of Kaiho, 1984b			R	R
Melonis	affinis (Reuss)		R	R	R
Melonis	elegans Kaiho			R	C
Melonis	lobatus Kaiho				R
Melonis	sp. cf. M. multisuturalis van Bellen				R
Melonis	pompilioides (Fitchell and Moll)	R	C	C	R
Melonis	subevolutus Kaiho			R	C
Nodogeneria	sp. cf. N. lepidula (Schwager)			R	C
Nodosaria	amchitkaensis (Todd)**				C
Nodosaria	longiscata d'Orbigny			R	C
Nonion	ezoensis Kaiho			R	C
Nonion	subangularis Kaiho			R	R
Nonion	takayanagii Kaiho			R	
Nonionella	japonica (Yokoyama)				R
Nonionella	mabutii Asano				R
Oolina	hexagona (Williamson)				C
Oolina	simplex Reuss				C
Oolina	sp. cf. O. globosa (Montagu)			R	R
Oolina	sp. A of Kaiho, 1984b				R
Planulina	poronaiensis Asano	R			
Plectofrondicularia	delicatula Kaiho				R
Plectofrondicularia	packardii Cushman and Schenck				C
Plectofrondicularia	smithi Kaiho				C
Plectofrondicularia	vaughani Cushman				R
Praeglobobulimina	pyrula (d'Orbigny)		R	R	R
Praeglobobulimina	ovata (d'Orbigny)			R	R
Praeglobobulimina	pupoides (d'Orbigny)			R	C
Procerolagena	sp. cf. P. gracillima (Sequenza)			R	R
Pseudonodosaria	conica (Neugeboren)	R	R	R	R
Pseudonodosaria	inflata (Costa)	R	R	R	C
Pseudopolyphorina	hokkaidoana Kaiho	R	R	R	
Pullenia	eocenica Cushman and Siegfus	R	R	R	?
Pullenia	salisburyi R. E. and K. C. Stewart		C	C	C
Saracenaria	ujiei Kaiho			R	R
Sigmoidella	pacifica Cushman and Ozawa	C	C	C	C
Sigmomorphina	schenckii Cushman and Ozawa			C	C
Sigmomorphina	sp. A of Kaiho, 1984b				R
Stilosomella	sp. cf. S. japonica (Ishiwada)				R
Trifarina	hannai (Beck)			C	C
Uvigerina	ombetsuensis Kaiho				R
Valvulinella	lymani (Yokoyama)			R	R

**Figure 6.** Paleobathymetric distribution of benthic foraminifera. Data of Asano (1952), Ujiié and Watanabe (1960) and Kaiho (1984a, b) are also interpreted by the present study. R = Rare; C = Common; A = Abundant. Occurrences of species shown in boldface are supposed to be important for paleobathymetric interpretations. Occurrences of species with \* are restricted in the Utsunai Formation (Kaiho, 1984b), and with \*\* to the Omagari Formation (Asano, 1952; Kaiho, 1984b).

zones (B-C and H-I) and foraminiferal assemblage zones indicated by Kaiho (1984a; Figure 5), it is obvious that foraminiferal assemblage zones F5 and F7 (Kaiho, 1984a, c) were deposited in the upper bathyal zone. The foraminiferal assemblages of these zones contain abundant

*Bulimina schwageri* and *Angulogerina hannai* (Kaiho, 1984a, c) as well as numerous calcareous foraminifera such as *Gyroidina yokoyamai* and *Plectofrondicularia packardii*. These latter two species were not encountered in the Yufutsu-Umaoi district and therefore must represent the



Eocene upper bathyal zone.

Paleobathymetric distributions of benthic foraminifera in the Poronai Sea are summarized in Figure 6 based on the present study and compilation of previous reports (Asano, 1952; Ujiié and Watanabe, 1960; Kaiho, 1984a, b).

#### Paleoenvironmental implications of abundant agglutinated foraminifera

The paleobathymetric distributions of benthic foraminifera in the study area indicate that the shallower marine assemblages include higher abundances of agglutinated foraminifera. Because similar assemblages dominated by agglutinated foraminifera have not been reported from other coastal regions of the North Pacific while various calcareous species have been reported (e.g. Ingle, 1980; McDougall, 1980), a local environmental factor is considered to have controlled the distribution.

Greiner (1970) proposed that availability of calcium carbonate for test construction is the controlling environmental factor in the distribution of calcareous foraminifera. In environments where calcium carbonate availability is insufficient for calcareous foraminifera, agglutinated foraminifera dominate. Examples of environments with insufficient calcium carbonate are found in brackish coastal areas, estuaries, and marshes (e.g., Zalesny, 1959; Bandy and Arnal, 1960; Anderson, 1963; Scott *et al.*, 1983; Zheng and Fu, 1992). Highly diverse agglutinated foraminiferal associations are also reported from the Arctic Ocean, in areas affected by the brackish surface water (Vilks, 1969; Hunt and Corliss, 1993; Schröder-Adams *et al.*, 1990).

Based on these modern examples of foraminiferal ecology, abundant occurrences of agglutinated foraminifera from the Ishikari Group and the Poronai Formation are thought to be the result of deposition in areas under the influence of brackish surface-water.

#### Water stratification

Previous studies on the lithostratigraphy and dinoflagellate assemblages showed that water stratification was important in the basal part of the Poronai Formation (Matsuno *et al.*, 1964; Kurita and Matsuoka, 1994). Previous studies also supposed that the Poronai Formation was deposited in an embayment called the "Poronai Sea" (Teshima, 1967; = "Paleo-Poronai Sea" of Kaiho, 1983, 1984c). This interpretation is mainly based on the geographical distribution of the Poronai Formation and its equivalents (Figure 1A). Absence or rare occurrences of planktonic foraminifera and radiolarians in the Yufutsu-Umaoi district indirectly support this interpretation. Such closed paleogeography may be an important factor for the water stratification.

According to Kaiho (1984a, b), Teshima (1955)'s megafossil zone A, found in the basal part of the Poronai

Formation, corresponds approximately to the foraminiferal zones from the *Haplophragmoides tanaii*-*Haplophragmoides subevolatus* Assemblage Zone to the *Haplophragmoides umbilicatus*-*H. subevolatus* Assemblage Zone of Kaiho (1984a, c; Figure 5). Accounting for the synonyms discussed in the taxonomic section below, species composition of Kaiho's zones is similar to the *Evolutinella subamakusaensis*-*Haplophragmoides crassiformis* Assemblage Zone and the *Globocassidulina globosa*-*Criboelphidium sorachiense* Assemblage Zone of the Yufutsu-Umaoi district. This similarity shows that the stratigraphic interval from the *H. tanaii*-*H. subevolatus* Assemblage Zone to the *H. umbilicatus*-*H. subevolatus* Assemblage Zone in the Yubari district was deposited under paleobathymetric conditions within, or shallower than, the middle sublittoral zone of the Yufutsu-Umaoi district.

Matsuno *et al.* (1964) also pointed out that the megafossil zone A defined by Teshima (1955), at the basal part of the Poronai Formation in the Yubari coal field, is rich in organic carbon and presumably was deposited in an oxygen-depleted paleoenvironment.

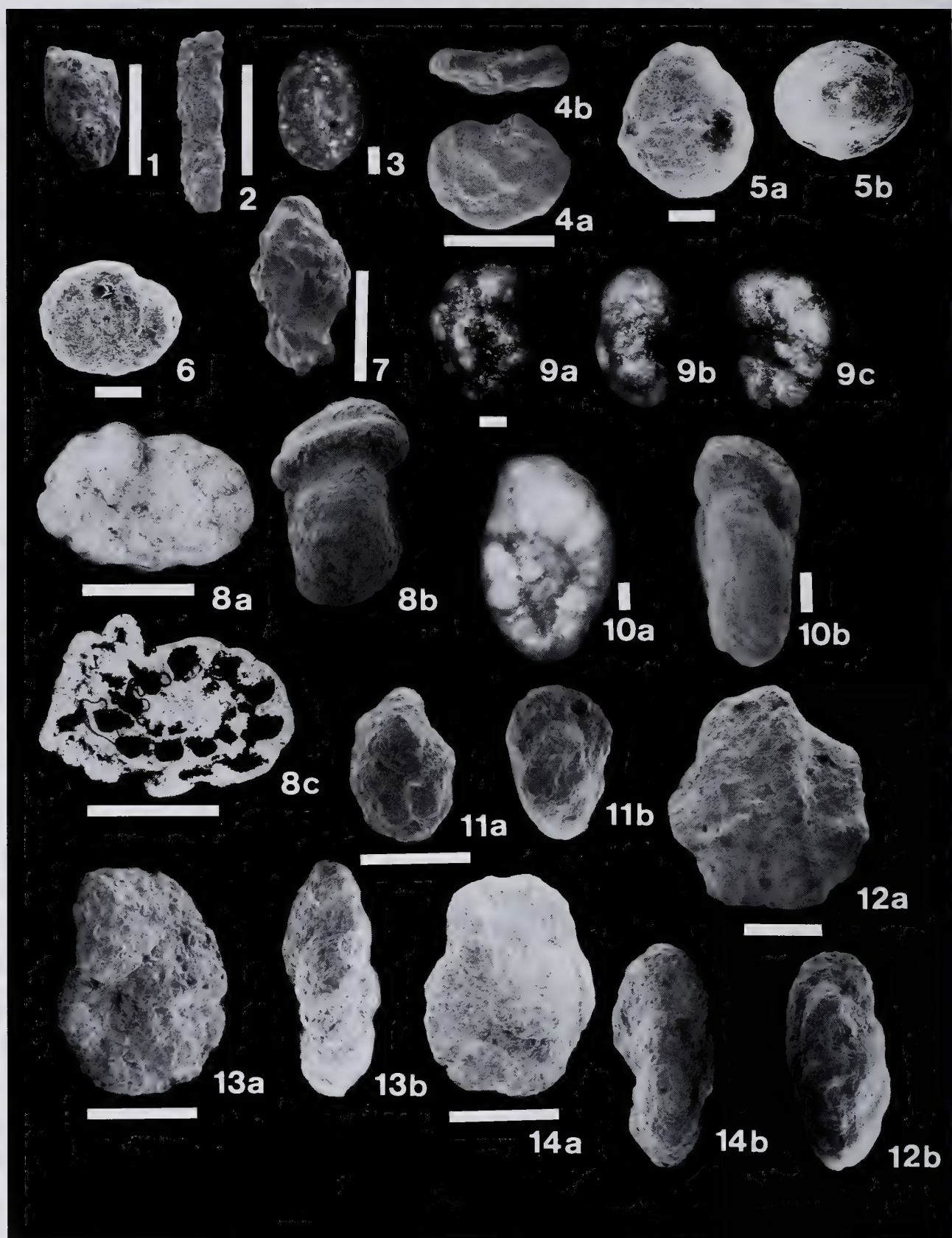
Based on these lines of evidence, sediments deposited in stratified shallow marine water masses are widely distributed in the Poronai Formation of the Yufutsu-Umaoi district and the Yubari district. These stratified water masses are believed to have formed as a result of fresh water input, as suggested by the dominant agglutinated foraminifers. In such an environment, a decreasing supply of dissolved oxygen from the sea surface may have caused oxygen depletion in substratum due to degradation of organic matter, as commonly observed in modern shallow marine areas (Tyson and Pearson, 1991).

#### Conclusion

Three Eocene foraminiferal assemblage zones, *Evolutinella subamakusaensis*-*Haplophragmoides crassiformis* Assemblage Zone, *Globocassidulina globosa*-*Criboelphidium sorachiense* Assemblage Zone and *Bulimina schwageri*-*Angulogerina hannai* Assemblage Zone, in ascending order, were defined in the well sections of the Yufutsu-Umaoi district, southern central Hokkaido. Assemblages characterizing each assemblage zone indicate the littoral to inner sublittoral zone, the middle sublittoral zone and the outer sublittoral zone, respectively.

Furthermore, compositions of foraminiferal assemblages of the Eocene upper bathyal zone were described based on a reevaluation of the previous studies. The upper bathyal zone is characterized by occurrence of abundant calcareous species such as *Gyroidina yokoyamai* and *Plectofrondicularia packardii*.

Abundant occurrences of agglutinated foraminifera suggest brackish-water paleoenvironments caused by fresh-





water input. Such brackish water may cause stratification and resultant oxygen depletion.

As a result of the present study, compositions of Eocene shallow marine foraminiferal assemblages in northern Japan were revealed. These data are expected to form a basis for considering the geohistory of the Paleogene formations in Hokkaido, as well as the paleoceanography of the northwestern Pacific region during the Eocene.

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### Taxonomic notes

Species which occurred in the Yufutsu-Umaoi district are arranged in taxonomic order following Loeblich and Tappan (1987). For the present identification, topotype, ideotype and hypotype specimens collected by K. Kaiho and presently deposited in JAPEx Research Center, Chiba, Japan, were compared. Because of poor preservation of the specimens, no new species were described herein, although several synonymies are discussed. All figured specimens are deposited in the collection of JAPEx Research Center.

#### *Bathysiphon eocenica* Cushman and Hanna (Figure 7.1)

*Bathysiphon eocenica* Cushman and Hanna, 1927, p. 210, pl. 13, figs. 2, 3. —Asano, 1952, p. 31, pl. 3, figs. 3, 4. —Ujiié and Watanabe, 1960, p. 127, pl. 1, figs. 3, 4. —Fukuta, 1962, p. 7, pl. 1, fig. 1. —Kaiho, 1984b, p. 42, pl. 1, figs. 3a, b. —Kaiho, 1992b, p. 365, pl. 1, fig. 1, pl. 5, fig. 1, 2.

#### *Bathysiphon vernoni* Hamlin (Figure 7.2)

*Bathysiphon vernoni* Hamlin, 1963, p. 153, pl. 14, figs. 1a–2b. —Kaiho, 1984b, p. 42, pl. 1, fig. 4.

#### *Placentammina* sp. A (Figure 7.5, 7.6)

**Description.**—Test free, small, unilocular, pyriform; very finely agglutinated and almost transparent; aperture round opening at the top of pyriform shell with very short projection.

**Remarks.**—Almost all of the specimens were deformed secondarily.

#### *Reophax tappuensis* Asano (Figure 7.7)

*Reophax tappuensis* Asano, 1958, p. 71, pl. 13, figs. 8, 9. —Kaiho, 1984b, pl. 1, figs. 10a–12.

#### *Cribrostomoides* sp. cf. *C. cretacea* Cushman and Goudkoff (Figure 7.11, 7.12)

Cf. *Cribrostomoides cretacea* Cushman and Goudkoff, 1944, p. 54, pl. 9, figs. 4a, b.

**Remarks.**—All specimens are so distorted that accurate identification is difficult. Coiling planes are always tilted to show very weak streptospiral involute coiling, therefore this form must be assigned to genus *Cribrostomoides* following Jones *et al.* (1993). It is distinguishable from allied species in its involute coiling, six to eight inflated chambers in final whorl, finely agglutinated and slightly transparent wall.

#### *Evolutinella subamakusaensis* (Fukuta) (Figure 8.10–8.12)

*Cribrostomoides* cf. *cretacea* Cushman and Goudkoff. —Ujiié and Watanabe, 1960, p. 127, pl. 1, figs. 3–5.

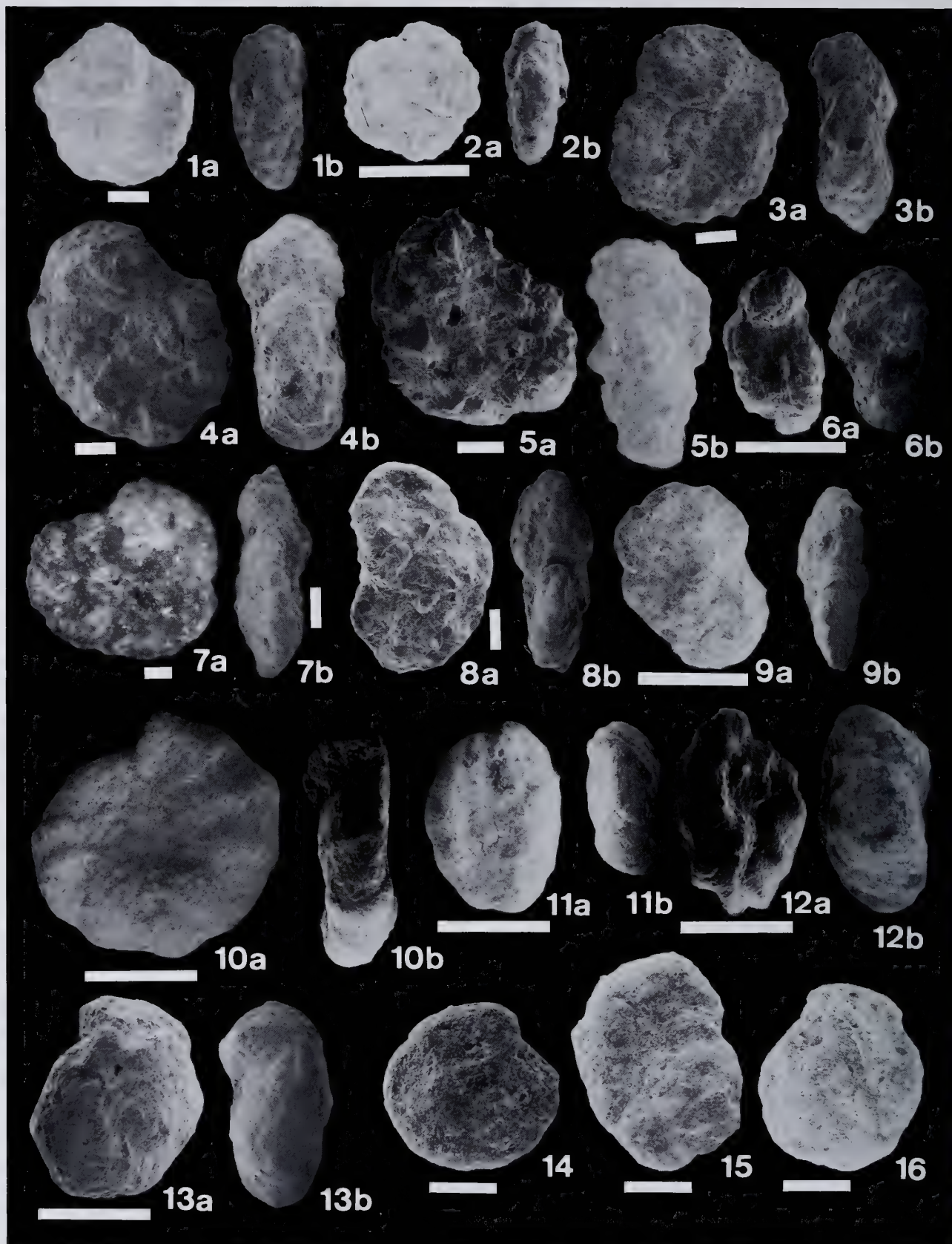
*Haplophragmoides subamakusaensis* Fukuta, 1962, p. 9, fig. 2, pl. 1, figs. 6–10.

*Haplophragmoides subevolutus* Kaiho, 1984a, p. 114, pl. 7, figs. 7a, b. —Kaiho, 1992c, pl. 1, figs. 8a, b.

*Cribrostomoides* sp. A. Yasuda, 1986, p. 51, pl. 3, figs. 9a, b.

**Description.**—Test free, planispirally enrolled, frequently coiling plane is unstable and sometimes show streptospiral appearance, slightly to completely evolute;

◀ **Figure 7.** Foraminifera from the Poronai Formation and Ishikari Group appearing in the wells studied. Scale bars equal 100  $\mu$ m except figs. 1, 2, 4, 7, 8, 11, 12, 13, and 14, where bars equal 500  $\mu$ m. **1.** *Bathysiphon eocenica* Cushman and Hanna, from MITI Umaoi, 3840 m. **2.** *Bathysiphon vernoni* Hamlin, from Kita-Akebono SK-1D, 3580 m. **3.** *Ammodiscus* sp., from Numanohata SK-4D, 3600 m. **4a, b.** *Glomospira* sp., from Numanohata SK-4D, 3305 m. **5a, b.** *Placentammina* sp. A, from Kita-Akebono SK-1D, 3330 m. **6.** *Placentammina* sp. A, from Kita-Akebono SK-1D, 3310 m. **7.** *Reophax tappuensis* Asano, from Kita-Akebono SK-1D, 3320 m. **8a, c.** *Budashevaella* sp. aff. *B. multicamerata* (Voloshinova), from MITI Umaoi, 4000 m. **9a–c.** *Budashevaella symmetrica* (Ujiié and Watanabe), from Numanohata SK-4D, 3240 m. **10a, b.** *Budashevaella symmetrica* (Ujiié and Watanabe), from MITI Umaoi, 3720 m. **11a, b.** *Cribrostomoides* sp. cf. *C. cretacea* Cushman and Goudkoff, from Numanohata SK-4D, 3340 m. **12a, b.** *Cribrostomoides* sp. cf. *C. cretacea* Cushman and Goudkoff, from Kita-Akebono SK-1D, 3250 m. **13a, b.** *Haplophragmoides crassiformis* Kaiho, from Numanohata SK-4D, 3660 m. Specimen bilaterally compressed by secondary deformation. **14a, b.** *Haplophragmoides crassiformis* Kaiho, from Kita-Akebono SK-1D, 3640 m.





biumbilicate; chambers inflated, 7–12 in final whorl; wall thin, finely agglutinated, exterior smoothly finished; aperture interiomarginal.

**Remarks.**—This species is assigned to the genus *Evolutinella* because of its evolute planispiral coiling. It is also characterized by numerous chambers and finely agglutinated wall. Ujiie and Watanabe (1960) first reported this species from the Poronai Formation as *Cribrostomoides* cf. *cretacea* Cushman and Goudkoff. Subsequently, Fukuta (1962) included the form in the synonymy of his *Haplophragmoides subamakusaensis* described from the Kyoragi Formation of the Amakusa Islands, Kyushu, and noted that this species was found also from the Poronai, Akabira and Wakkanabe Formations of the Ishikari Coal field. Later, Kaiho (1984a) described *H. subevolutus* from the Poronai Formation and synonymized *C.* cf. *cretacea* of Ujiie and Watanabe (1960) without reference to the study of Fukuta (1962). *H. subamakusaensis* and *H. subevolutus* have quite similar morphology and are regarded here as synonyms. Kaiho and Nishi (1989) reported *H. subevolutus* from the Middle Eocene to Early Oligocene Hyuga Group in southern Kyushu without any figures. Thus it is obvious that *E. subamakusaensis* has a broad geographic distribution from Hokkaido to Kyushu, and a long stratigraphic range from the Maastrichtian to lower Oligocene. Kaiho (1984a) included the specimens having numerous chambers, up to 14, in the final whorl in *H. subevolutus*. However, I did not find specimens having more than 13 chambers in the present study. In Figures 8–12, specimens collected from the Kyoragi Formation (not topotypes but collected from near the type locality) are shown for comparison.

*Haplophragmoides crassiformis* Kaiho (Figure 7.13, 7.14)

*Haplophragmoides* cf. *emaciata* (Brady). —Ujiie and Watanabe, 1960, p. 127, pl. 1, figs. 6a, b.

*Haplophragmoides crassiformis* Kaiho, 1984a, p. 114, pl. 7, figs. 3a, b.

*Haplophragmoides rugosus soyaensis* Yasuda (Figure 8.3, 8.4)

*Haplophragmoides rugosus soyaensis* Yasuda, 1986, p. 50, pl. 5, figs. 5a–7c.

*Haplophragmoides umbilicatus* Kaiho, 1984a, p. 115, pl. 7, figs. 6a, b. (non *Haplophragmoides umbilicatus* Pearcey).

*Haplophragmoides apertiumbilicatus* Kaiho, 1986, nom. nov.

**Remarks.**—This species is characterized by its deeply depressed umbilicus, seven inflated chambers in the final whorl, and compact arrangement of chambers. Distinguished from *H. amakusaensis* Asano in possessing curved sutures.

*Haplophragmoides tanaii* Kaiho (Figure 8.5)

*Haplophragmoides tanaii* Kaiho, 1984a, p. 115, pl. 7, figs. 5a, b.

**Remarks.**—This species is characterized by its small test size, coarsely agglutinated wall, and subacute periphery. *H. kushiroensis* Asano (1962) described from the Paleogene of eastern Hokkaido has similar morphology in its test size, number of chambers, acute periphery and coarsely agglutinated wall but is supposed to be distinguished by possessing curved sutures.

*Haplophragmoides yokoyamai* Kaiho (Figure 8.1, 8.2)

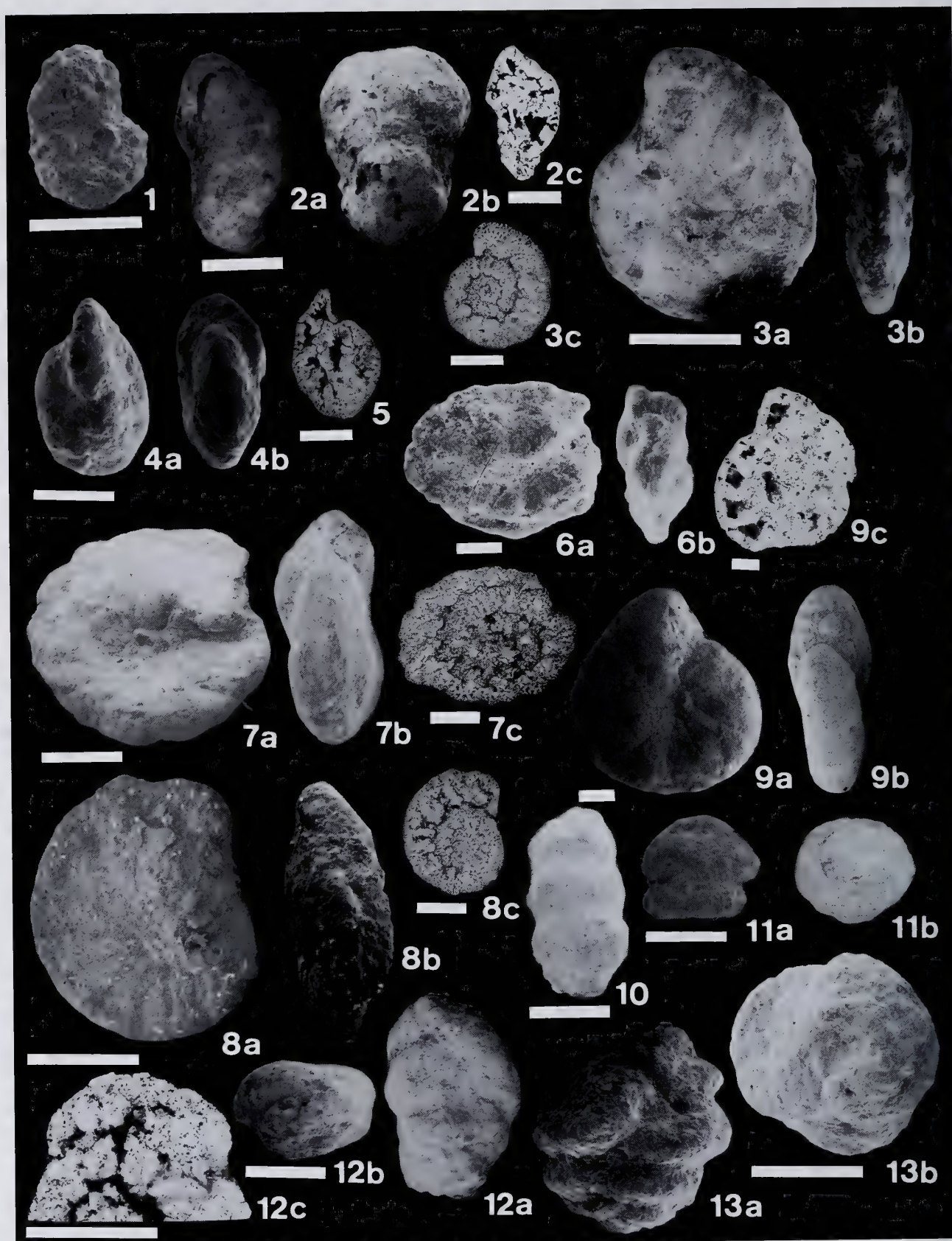
*Haplophragmoides kirki* Wickenden; Mallory, 1959, p. 112, pl. 2, figs. 8a, b. —Takayanagi, 1960, p. 72, pl. 2, figs. 3a, b.

*Haplophragmoides yokoyamai* Kaiho, 1984a, p. 116, pl. 7, figs. 4a, b.

**Remarks.**—Mallory (1959) first reported this species as *H. kirki* from the Eocene of California. Takayanagi (1960) also reported this species from the Albian to Campanian of Hokkaido as *H. kirki*. Later Kaiho (1984a) described *H. yokoyamai* from the Poronai Formation as new. The holotype of *H. kirki* from the Cretaceous of North America (Wickenden, 1932, p. 85, pl. 1, fig. 1) shows a smaller test, broadly rounded periphery and more finely agglutinated wall compared to *H. yokoyamai*. Furthermore, specimens of Mallory (1959) and Takayanagi (1960) have a compressed test, larger test size and a coarser wall than typical *H. kirki*. Moreover, *H. kirki* is synonymized to *H. excavata* Cushman and Walters by Mello (1971), who added that *H. excavatus* shows such a wide range of morphological variation that *H. kirki* falls within the range of variation of the

◀ **Figure 8.** Foraminifera from the Poronai Formation and Ishikari Group appearing in the wells studied. Specimens shown for comparison in Figure 12a, b were collected from the Kyoragi Formation. Scale bars equal 100  $\mu$ m except figs. 2, 6, 9, 10, 11, 12, and 13, where bars equal 500  $\mu$ m. **1a, b.** *Haplophragmoides yokoyamai* Kaiho, from MITI Umaoi, 3840m. Medium-sized specimen. **2a, b.** *Haplophragmoides yokoyamai* Kaiho, from MITI Umaoi, 3840 m. Largest-size specimen. **3a, b.** *Haplophragmoides rugosus soyaensis* Yasuda, from MITI Umaoi, 4160 m. **4a, b.** *Haplophragmoides rugosus soyaensis* Yasuda, from MITI Umaoi, 4160 m. **5a, b.** *Haplophragmoides tanaii* Kaiho, from MITI Umaoi, 4000 m. **6a, b.** *Haplophragmoides* sp. A, from Numanohata SK-4D, 3110 m. **7a, b.** *Haplophragmoides* sp. B, from MITI Umaoi, 4060 m. **8a, b.** *Haplophragmoides* sp. B, from Kita-Akebono SK-1D, 3350 m. **9a, b.** *Haplophragmoides* sp. D, from MITI Umaoi, 3820 m. **10a, b.** *Evolutinella subamakusaensis* (Fukuta), from Numanohata SK-4D, 3600 m. Specimen bilaterally compressed by secondary deformation. **11a, b.** *Evolutinella subamakusaensis* (Fukuta), from Numanohata SK-4D, 3600 m. Specimen vertically compressed by secondary deformation. **12a, b.** *Evolutinella subamakusaensis* (Fukuta), from the Kyoragi Formation. Specimen vertically compressed by secondary deformation. **13a, b.** *Recurvoides* sp. A, from MITI Umaoi, 3920 m. **14–16.** *Recurvoidella* sp. cf. *R. lamella* (Grzybowski), all specimens from Numanohata SK-4D, 3500 m.







former species.

*Recurvoidella* sp. cf. *R. lamella* (Grzybowski) (Figure 8.14–8.16)  
Cf. *Trochammina lamella* Grzybowski, 1898, p. 290, pl. 11, fig. 25.

Cf. *Recurvoidella lamella* (Grzybowski). —Charnock and Jones, 1990, p. 173, pl. 6, figs. 11, 12, pl. 17, fig. 7; Kaminski and Geroch, 1993, p. 263–264, pl. 10, figs. 8, 9.

**Remarks.**—Most specimens are depressed almost completely.

*Budashevaella symmetrica* (Ujiie and Watanabe) (Figure 7.9, 7.10)

*Trochammina symmetrica* Ujiie and Watanabe, 1960, p. 134, pl. 1, figs. 10, 11.

**Description.**—Test free, medium, early stage compactly streptospiral; the angle between one coiling plane and subsequent one increases as growth proceeds, up to 90° in an adult form, the last whorl and half of the penultimate whorl are visible on the surface in a juvenile form, but the penultimate one becomes almost invisible in the adult, few chambers of penultimate whorl exposed in umbilical area; slightly evolute; chambers not inflated in earlier coil, become slightly inflated, seven to eight in final whorl, increasing slowly in size as added; sutures radial, slightly depressed, limbate; wall finely agglutinated, thick; aperture interiomarginal.

**Remarks.**—The streptospiral coiling of this species confirms the assignment to the genus *Budashevaella*. This species is similar to *Haplophragmoides subamakusaensis* Fukuta in general appearance but is distinguished by its less inflated chambers, less depressed sutures and streptospiral coiling. It is also distinguished from *Budashevaella* sp. aff. *B. multicamerata* of the present study in having fewer number of chambers in the final whorl.

*Budashevaella* sp. aff. *B. multicamerata* (Voloshinova) (Figure 7.8)

Aff. *Circus multicameratus* Voloshinova, in Voloshinova and Budasheva, 1961, p. 201, pl. 7, fig. 6, pl. 8, fig. 1.

*Budashevaella multicamerata* (Voloshinova). —McDougall,

1980, p. 34, pl. 3, figs. 4–6.

**Diagnosis.**—Numerous chambers up to 14 in final whorl. Coiling plane of the last coil lies at about a right angle to that of the penultimate one in the umbilical area.

**Remarks.**—This form is distinguished from *B. multicamerata* (Voloshinova), originally described as *Circus multicameratus* from the Neogene of Sakhalin, in its broadly rounded periphery.

*Reticulophragmium amakusaensis* (Fukuta) (Figure 9.9)

*Cyclammina amakusaensis* Fukuta, 1962, p. 12, text-figs. 3a–b, pl. 3, figs. 8–10.

**Description.**—Test free, medium, planispirally coiled and involute to very slightly evolute, 10–13 chambers in final whorl, whorls increasing rapidly in height; wall finely agglutinated; sutures depressed, straight and radial; slightly biumbilicate; aperture an interiomarginal equatorial slit.

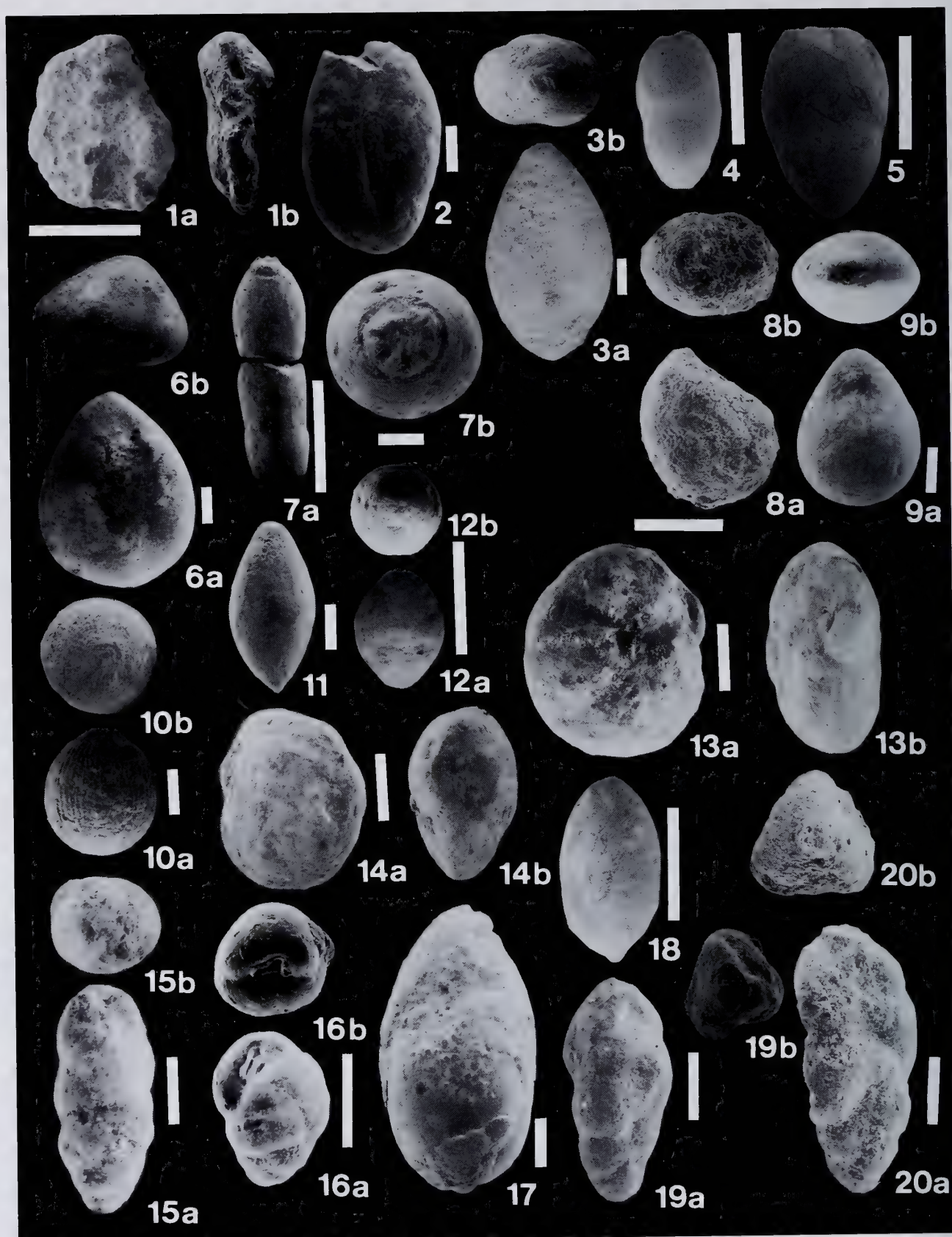
**Remarks.** This species was originally described from the Kyoragi Formation of the Amakusa Islands, Kyushu, as a species of *Cyclammina*. Because of the position of the aperture and reticulate wall, it is newly assigned to the current genus. Thin section showing a wide cavity in each chamber indicates that development of alveolar structure is quite weak (Figure 9.9c). It commonly occurred in the study sections, although it has never been recorded from the Poronai Formation in surface sections. It is highly possible that the present species has been assigned to other *Cyclammina* species by previous workers.

*Cyclammina ezoensis* Asano (Figure 9.3)

*Cyclammina ezoensis* Asano, 1951a, pl. 1, figs. 1a, b. —Asano, 1951b, p. 20, pl. 3, figs. 2a, b. —Ujiie and Watanabe, 1960, pl. 1, fig. 7. —Kaiho, 1984b, p. 45, 46, pl. 1, figs. 21a, b. —Kaiho, 1992b, p. 367, 368, pl. 1, figs. 5a, b.

**Remarks.**—This species is characterized by a compressed test with thin periphery. It was originally described from the Miocene Masuporo Formation in Hokkaido, and was commonly recovered from the Paleogene as well as Neogene formations of Japan. Neogene specimens sometimes attain much larger diame-

← **Figure 9.** Foraminifera from the Poronai Formation and the Ishikari Group appearing in the wells studied. Scale bars equal 100  $\mu$ m except figs. 1, 3, 4, 5, 7, 8, 10, 11, 12, and 13, where bars equal 500  $\mu$ m. **1.** *Ammobaculites* sp., from Kita-Akebono SK-1D, 3430 m. **2a–c.** *Alveolophragmium* sp. A, from MITI Umai, 3860 m. **3a–c.** *Cyclammina ezoensis* Asano, from MITI Umai, 4410 m. **4a, b.** *Cyclammina pacifica* Beck, from Kita-Akebono SK-1D, 3075 m. **5.** *Cyclammina pacifica* Beck, from Numanohata SK-4D, 3220 m. **6a, b.** *Cyclammina* sp. aff. *C. pusilla* Brady, from Kita-Akebono SK-1D, 3260 m. **7a–c.** *Cyclammina* sp., from Numanohata SK-4D, 3240 m. Note that this specimen has 15 chambers in the final whorl. **8a–c.** *Cyclammina* sp., from Numanohata SK-4D, 3760 m. Note that this specimen has 15 chambers and a bilaterally compressed test. **9a–c.** *Reticulophragmium amakusaensis* (Fukuta), from MITI Umai, 3740 m. **10.** “*Clavulina*” sp. from MITI Umai, 4060 m. **11a, b.** Fragment of last chamber of “*Clavulina*”-like species, from MITI Umai, 4060 m. Note the characteristic large cone-shaped last chamber. **12a–c.** *Poronaiia poronaiensis* (Asano), from Numanohata SK-4D, 3240 m. **13a, b.** *Poronaiia poronaiensis* (Asano), from Kita-Akebono SK-1D, 3210 m.





ters, as much as 4 mm, but commonly have fewer chambers in comparison with the Paleogene specimens.

***Cyclammina pacifica* Beck (Figure 9.4, 9.5)**

*Cyclammina pacifica* Beck, 1943, pl. 98, figs. 2, 3. —Asano, 1952, p. 33, pl. 3, figs. 1a, b, 2, pl. 5, figs. 11a, b. —Asano, 1958, pl. 13, fig. 3. —Kaiho, 1992b, p. 368, pl. 1, figs. 6a, b.

*Cyclammina* cf. *pacifica* Beck. —Asano, 1951a, p. 7, figs. 24, 25. —Asano, 1951b, p. 20–21, pl. 3, figs. 5a, b. —Fukuta, 1962, p. 11, pl. 3, figs. 1–3. —Kaiho, 1984b, p. 46, pl. 2, figs. 1a, b.

**Remarks.**—This species has been commonly recorded from various Neogene and Paleogene formations throughout Japan. It shows compact arrangement of chambers. Although alveolar structure is rather poorly developed in the figured specimen (Figure 9.5), degree of development of alveolar structure varies among specimens.

***Cyclammina* sp. aff. *C. pusilla* Brady (Figure 9.6)**

Aff. *Cyclammina pusilla* Brady, 1881, p. 53; Type figures: Brady, 1884, pl. 37, figs. 20–23.

*Cyclammina pusilla* Brady. —Kaiho, 1984b, p. 46, pl. 2, figs. 2a, b.

**Remarks.**—Specimens from the Poronai Formation have a smaller test size and subacute periphery, and are therefore distinguished from *C. pusilla*.

***Poronaiia poronaiensis* (Asano) (Figure 9.12, 9.13)**

*Plectina poronaiensis* Asano, 1952, p. 33, 34, pl. 4, figs. 12, 13. —Asano, 1958, pl. 13, figs. 5–7. —Fukuta, 1962, p. 16, pl. 5, figs. 4, 5.

*Poronaiia poronaiensis* (Asano). —Ujiié and Watanabe, 1960, p. 133, 134, pl. 2, figs. 1–8.

*Plectotrochammina poronaiensis* (Asano). —Loeblich and Tappan, 1964, p. 279. —Kaiho, 1984b, p. 48, pl. 2, figs. 10a–d.

**Description.**—Test free, short and broadly cylindrical, lower trochospiral in the early stage with four chambers,

later biserial, each chambers imbricating to penultimate chambers; chambers inflated; wall finely agglutinated but occasionally includes coarse grains, internally imperfect alveolar structure developed; aperture, interiomarginal opening.

**Remarks.**—Specimens were occasionally deformed considerably. Loeblich and Tappan (1964) regarded the genus *Poronaiia* as a junior synonym of *Plectotrochammina*, and later assigned both genera to their list of “Genera of Uncertain Status” (Loeblich and Tappan, 1987). However, *Poronaiia* should be included in the family Textulariellidae because of possessing alveoli-like labyrinthic structure inside the test, while both *Plectina* and *Plectotrochammina* have a simple wall.

***Trochammina* sp. cf. *T. asagaiensis* Asano (Figure 10.1)**

Cf. *Trochammina asagaiensis* Asano, 1949, p. 475, text-figs. 2a–4b.

*Trochammina asagaiensis* Asano. —Kaiho, 1984b, p. 47, pl. 2, figs. 5a–6b.

**Remarks.**—This species is characterized by its very low trochospiral and compressed test. However, specimens examined in this study and the specimens of Kaiho (1984b) show low trochospiral, obscure earlier whorls and inflated chambers compared to *T. asagaiensis*.

***Quinqueloculina seminula compacta* Seroa (Figure 10.2)**

*Quinqueloculina seminulum* (Linné) var. *compacta* Seroa, 1960, pl. 3, figs. 7a–c.

*Quinqueloculina weaveri* Rau. —McDougall, 1980, p. 37, pl. 5, figs. 5–7.

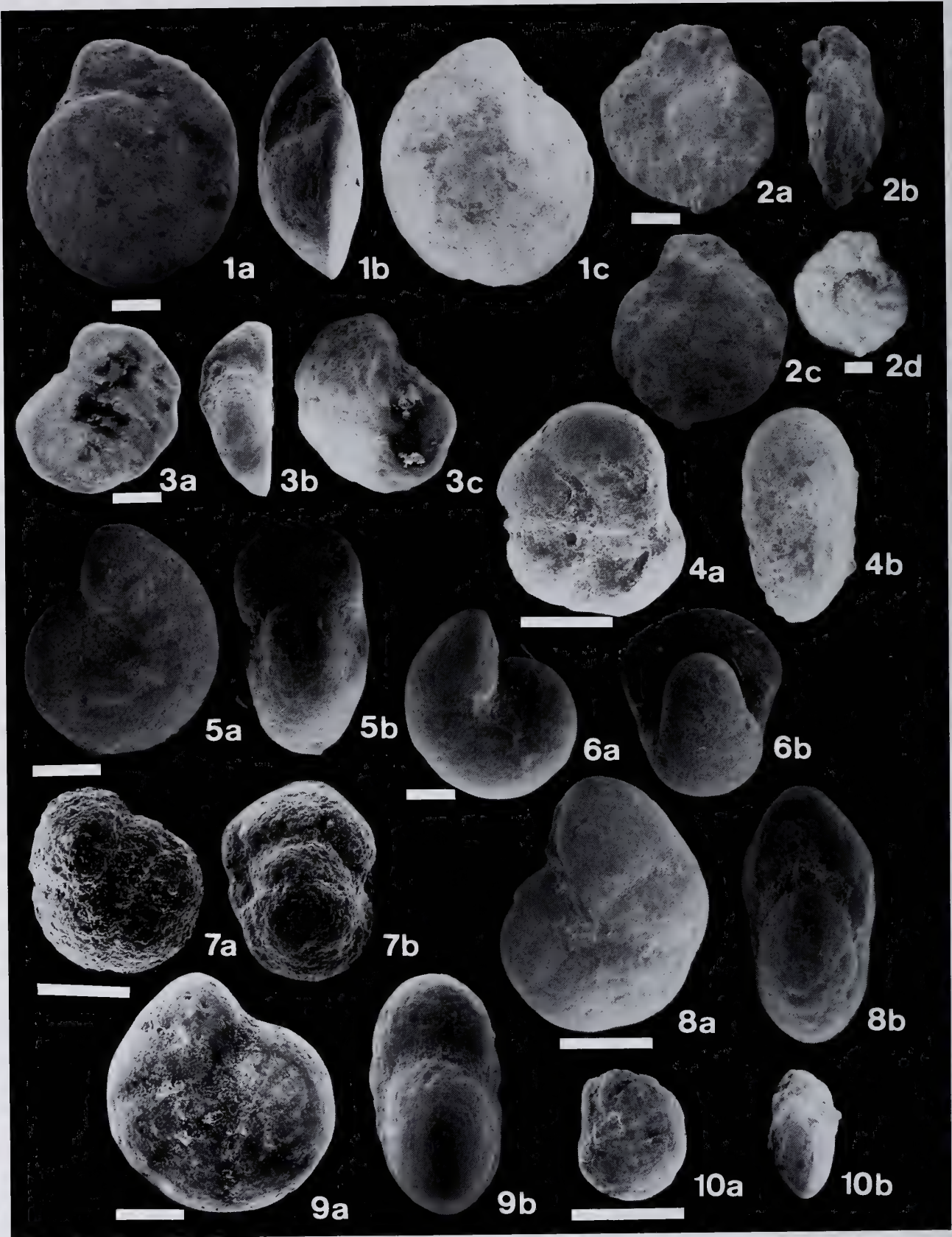
*Quinqueloculina* cf. *seminula compacta* Seroa. —Kaiho, 1984b, p. 49, pl. 2, figs. 12a–c.

***Dentalina* sp. cf. *D. subsoluta* (Cushman) (Figure 10.7)**

Cf. *Nodosaria subsoluta* Cushman, 1923, p. 74, pl. 13, fig. 1.

*Dentalina* cf. *subsoluta* (Cushman). —Kaiho, 1984b, p. 50–51, pl. 3, fig. 3. —Kaiho, 1992b, p. 373–374, pl. 1, fig. 14.

◆ **Figure 10.** Foraminifera from the Poronai Formation and Ishikari Group appearing in the wells studied. Scale bars equal 100  $\mu$ m except figs. 1, 4, 5, 7a, 12, and 18, where bars equal 500  $\mu$ m. **1a, b.** *Trochammina* sp. cf. *T. asagaiensis* Asano, from Numanohata SK-4D, 3220 m. **2.** *Quinqueloculina seminula compacta* Seroa, from Numanohata SK-4D, 3260 m. **3a, b.** *Guttulina takayanagii* Kaiho, from Numanohata SK 4D, 3460 m. **4.** *Pseudopolymorphina* sp. A, from Numanohata SK-4D, 3285 m. **5.** *Pseudonodosaria* sp. cf. *P. conica* (Neugeboren), from Numanohata SK-4D, 3305 m. **6a, b.** *Sigmoidella pacifica* (Cushman and Ozawa), from Numanohata SK 4D, 3400 m. **7a, b.** *Dentalina* sp. cf. *D. subsoluta* (Cushman), from Kita-Akebono SK-1D, 3360 m. **8a, b.** *Lenticulina* sp., from Kita-Akebono SK-1D, 3600 m. **9a, b.** *Fissurina* sp. cf. *F. marginata* (Montagu), from Kita-Akebono SK-1D, 3420 m. **10a, b.** *Lagena striata* (d'Orbigny), from MITI Umai, 3940 m. **11.** *Procerolagena* sp. cf. *P. gracilima* (Seguenza), from Kita-Akebono SK-1D, 3190 m. **12a, b.** *Glandulina laevigata ovata* Cushman and Applin, from Numanohata SK-4D, 3120 m. **13a, b.** *Globocassidulina globosa* (Hantken), from Numanohata SK-4D, 3240 m. **14a, b.** *Globocassidulina globosa* (Hantken), from Numanohata SK-4D, 3120 m. **15a, b.** *Bulimina schwageri* Yokoyama, from Numanohata SK-4D, 3120 m. **16a, b.** *Bulimina schwageri* Yokoyama (juvenile form), from Kita-Akebono SK-1D, 3120 m. **17.** *Globobulimina* sp., from MITI Umai, 4120 m. **18.** *Praeglobobulimina pyrula* (d'Orbigny), from Numanohata SK-3D, 3720 m. **19a, b.** *Angulogerina hannai* Beck, from MITI Umai, 3700 m. **20a, b.** *Angulogerina*





*Pseudonodosaria* sp. cf. *P. conica* (Neugeboren) (Figure 10.5)  
 Cf. *Pseudonodosaria conica* (Neugeboren). —McDougall, 1980, p. 36, pl. 9, figs. 7, 8. —Kaiho, 1992b, p. 374, figs. 17a, b.  
 Cf. *Pseudoglandulina obtusissima* (Reuss). —Yoshida, 1957, p. 64, text-figs. 3–9.  
 Cf. *Pseudonodosaria shitakaraensis* Kaiho, 1984a, p. 118, pl. 8, figs. 1a, b.

*Lagena striata* (d'Orbigny) (Figure 10.10)  
*Oolina striata* d'Orbigny, 1839, p. 21, pl. 5, fig. 12.  
*Lagena becki* Sullivan. —McDougall, 1980, p. 35, pl. 7, figs. 1, 4.  
*Lagena striata* (d'Orbigny). —Kaiho, 1984b, p. 51, 52, pl. 3, figs. 13a, b. —Kaiho, 1992b, p. 377, pl. 2, fig. 7.

*Lagena* sp. cf. *L. laevis* (Montagu)  
 Cf. *Vermiculum laeve* Montagu, 1803, p. 524; Type figure: Walker and Boys, 1784, pl. 1, fig. 9, as *Serpula* (*Lagena*) *laevis ovalis*.  
*Lagena laevis* (Montagu). —Kaiho, 1984b, p. 51, pl. 3, figs. 11–13.

**Remarks.**—Specimens of this study have similar features to those of Kaiho (1984b), but are distinguished from the Recent *L. laevis* in its shorter test.

*Procerolagena* sp. cf. *P. gracillima* (Seguenza) (Figure 10.11)  
 Cf. *Amphorina gracillima* Seguenza, 1862, p. 51, pl. 1, fig. 37.  
*Lagena gracillima* (Seguenza). —Kaiho, 1984b, p. 51, pl. 3, figs. 10a, b.  
 Cf. *Procerolagena gracillima* (Seguenza). —Jones, 1994, p. 62, figs. 19–22, 24–29.

**Remarks.**—This species is quite similar to *L. gracillima* of Kaiho (1984b), but different from the Recent *P. gracillima* in its shorter test.

*Guttulina takayanagii* Kaiho (Figure 10.3)  
*Guttulina takayanagii* Kaiho, 1984a, p. 120, pl. 8, figs. 5a–d.

*Pseudopolymorphina hokkaidoana* Kaiho  
*Pseudopolymorphina hokkaidoana* Kaiho, 1984a, p. 120, figs. 8a–c.

*Sigmoidella pacifica* (Cushman and Ozawa) (Figure 10.6)

*Guttulina* (*Sigmoidina*) *pacifica* Cushman and Ozawa, 1928, p. 19, pl. 2, fig. 13.

*Guttulina* cf. *pacifica* Cushman and Ozawa. —Fukuta, 1962, p. 23, pl. 7, figs. 9–10.

*Sigmoidella pacifica* Cushman and Ozawa. —Kaiho, 1984b, p. 58, fig. 53, pl. 4, figs. 12a–d.

**Remarks.**—This species is known from the Eocene formations from Kyushu to Hokkaido. It is common in the shallow marine facies in the lower part of the Poronai Formation, as discussed earlier. Since *S. pacifica* is also known from Recent shallow marine environments, it appears not to have changed habitat from the Eocene until the Recent. Although Jones (1994) regarded this species as a junior synonym of *Polymorphina elegantissima* Parker and Jones, I think these two species are distinguishable in the aspect of number of chambers visible from the the outside of the test.

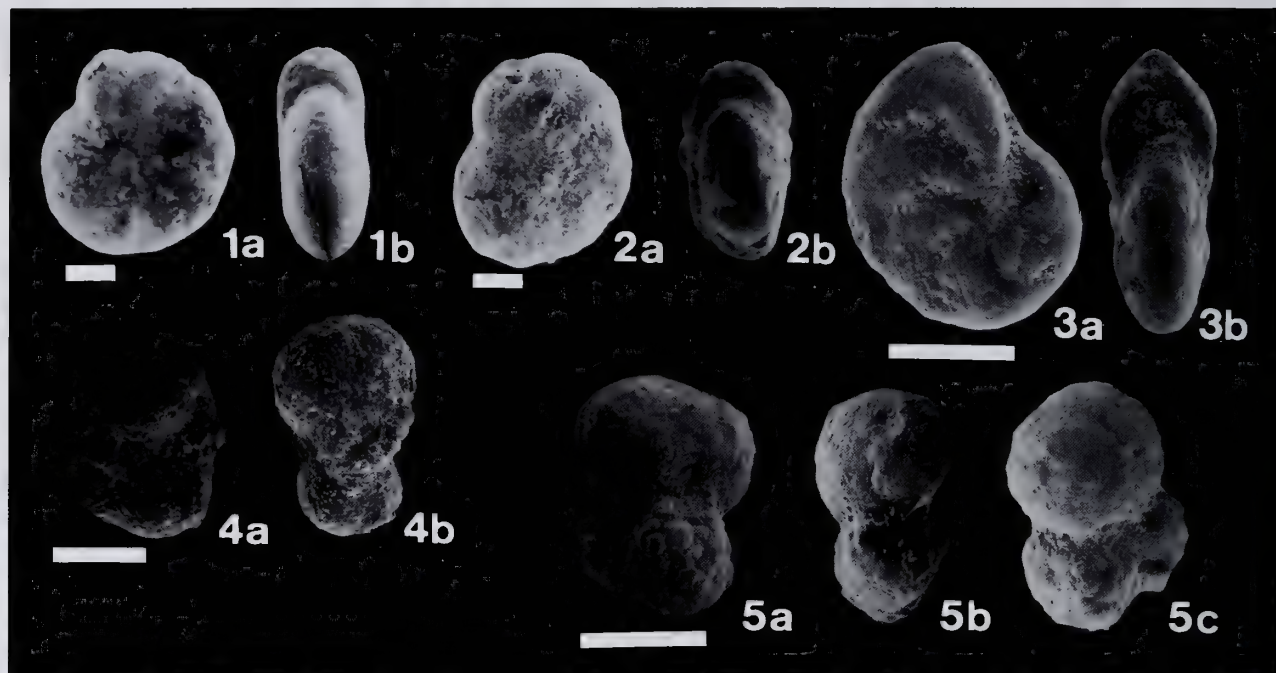
*Fissurina* sp. cf. *F. marginata* (Montagu) (Figure 10.9)  
 Cf. *Vermiculum marginatum* Montagu, 1803, p. 524; Type figure: Walker and Boys, 1784, pl. 1, fig. 7.  
 Cf. *Fissurina marginata* (Montagu). —Loeblich and Tappan, 1953, p. 77, pl. 14, figs. 6–9.

*Glandulina laevigata ovata* Cushman and Applin (Figure 10.12)  
*Nodosaria* (*Glandulina*) *laevigata* d'Orbigny var. *ovata* Cushman and Applin, 1926, p. 443, pl. 7, figs. 12, 13.  
*Glandulina laevigata ovata* Cushman and Applin. —Ujiié and Watanabe, 1960, p. 129, 130, pl. 2, figs. 11, 12. —Kaiho, 1984b, pl. 4, figs. 15a–c.

*Globocassidulina globosa* (Hantken) (Figure 10.13, 10.14)  
*Cassidulina globosa* Hantken, 1875, p. 64, pl. 16, fig. 2.  
*Globocassidulina globosa* (Hantken). —Kaiho, 1992b, p. 378, pl. 2, figs. 11a, b, pl. 5, figs. 17a, b.

*Bulimina schwageri* Yokoyama (Figure 10.15, 10.16)  
*Bulimina schwageri* Yokoyama, 1890, p. 190, pl. 24, figs. 6–8. —Ujiié and Watanabe, 1960, pl. 2, figs. 16, 17, 18. —Kaiho, 1984b, p. 62–63, pl. 5, figs. 11–15. —Kaiho, 1992b, p. 379, pl. 3, figs. 2a, b.  
*Caucasina schwageri* (Yokoyama). —Serova, 1976, p. 324, 325, pl. 1, figs. 6a–c.

➦ **Figure 11.** Foraminifera from the Poronai Formation and Ishikari Group appearing in the wells studied. Scale bars equal 100  $\mu$ m except fig. 10 where bar equals 500  $\mu$ m. **1a–c.** *Heterolepa poronaiensis* Kaiho, from Kita-Akebono SK-1D, 3340 m. **2a–d.** *Cibicides elmaensis* Rau, from Numanohata SK-3D, 3720 m. **3a, c.** *Cibicides* sp. A, from Kita-Akebono SK 1D, 3540 m. **4a, b.** *Nonionella japonica* (Yokoyama), from MITI Umai, 4000 m. **5a, b.** *Melonis affinis* (Reuss), from Numanohata SK-4D, 3340 m. **6a, b.** *Melonis pompilioides* (Fichtel and Moll), from Numanohata SK-4D, 3260 m. **7a, b.** *Pullenia eocenica* Cushman and Siegfus, from MITI Umai, 3980 m. **8a, b.** *Pullenia salisburyi* R. E. and K. C. Stewart, from Numanohata SK-4D, 3240 m. **9a, b.** *Criboelphidium sorachiense* (Asano), from Numanohata SK-3D, 3720 m. **10a, b.** *Criboelphidium ishikariense* (Kaiho), from Numanohata SK-3D, 3800 m.



**Figure 12.** Foraminifera from the Poronai Formation and Ishikari Group appearing in the wells studied. Scale bars equal 100  $\mu$ m. **1a, b.** *Criboelphidium wakkanabense* (Kaiho), from Numanohata SK-4D, 3240 m. **2a, b.** *Criboelphidium wakkanabense* (Kaiho), from Numanohata SK-3D, 3700 m. **3a, b.** *Criboelphidium* sp. from Kita-Akebono SK-1D, 3410 m. Note that this specimen shows subacute periphery. **4a, b.** Planktonic foraminifera genus and species indeterminable. from MITI Umaoi, 4120 m. **5a-c.** *Subbotina* sp., from Kita-Akebono SK-1D, 3440 m.

**Remarks.** — This species has been recorded from Hokkaido to Kamchatka. As discussed by Kaiho (1984b), *B. schwageri* has three to four chambers in the first whorl, and is distinguished from the species of *Caucasina* which always have four chambers in the final whorl. Even if there is a phylogenetic relationship between *B. schwageri* and *Caucasina* species as pointed out by Serova (1976), emendation by reexamination of the type species of the genus *Caucasina* is necessary.

***Praeglobobulimina pyrula* (d'Orbigny) (Figure 10.18)**

*Bulimina pyrula* d'Orbigny, 1846, p. 184, pl. 11, figs. 9, 10.  
—Asano, 1952, p. 41, figs. 10a, b. —Kaiho, 1984b, p. 62, pl. 5, figs. 10a-c.

***Praeglobobulimina* sp. cf. *P. ovata* (d'Orbigny)**

Cf. *Bulimina ovata* d'Orbigny, 1846, p. 185, pl. 11, figs. 13, 14.  
*Praeglobobulimina ovata* (d'Orbigny). —Kaiho, 1984b, pl. 6, fig. 2. —Kaiho, 1992b, pl. 3, fig. 5.

***Angulogerina hannai* Beck (Figure 10.19, 10.20)**

*Angulogerina hannai* Beck, 1943, p. 607, pl. 108, figs. 26, 28.  
*Trifarina cushmani* Todd and Knifer, 1952, p. 23, pl. 4, figs. 6a, b.  
*Trifarina maiyai* Kaiho, 1984a, p. 122, 123, pl. 9, figs. 7a, b.

*Trifarina hannai* (Beck). —Kaiho, 1992b, p. 380, pl. 3, figs. 7a, b.

**Remarks.** — Relationship between *T. maiyai* and *T. hannai* follows the study of Kaiho (1992b). *T. cushmani* was originally reported from the Eocene in Chile and also reported from the Poronai Formation by Maiya (1979). Although Maiya (1979) did not figure any specimens, observation of his specimens by the present author revealed that they are conspecific with *A. hannai*. I regard *T. cushmani* as a junior synonym of *A. hannai* because of their similarity in morphology, such as test size and subacute periphery, on the basis of the original illustration by Todd and Knifer (1952).

***Cibicides elmaensis* Rau (Figure 11.2)**

*Cibicides elmaensis* Rau, 1948, p. 173, pl. 31, figs. 18-26.  
—Fukuta, 1962, p. 25, pl. 8, figs. 3a, b, 7a, b.  
*Cibicides biconbexus* Kaiho, 1984a, p. 124, pl. 9, figs. 7a-c.  
? *Cibicides yabei* Asano, 1952, p. 43, pl. 4, figs. 1a-c.

**Remarks.** — *Cibicides yabei* Asano (1952) was described from the basal part of the Poronai Formation, but was not recorded by Kaiho (1984a, b) who studied the same formation in the same area. As discussed by Asano (1952), *C.*



*yabei* is distinguished from *C. elmaensis* in lacking shell material filling the umbilical area, but I think that this is insufficient to separate *C. yabei* as a different species.

***Nonionella japonica*** (Yokoyama) (Figure 11.4)

*Pilvulineria japonica* Yokoyama, 1890, p. 192, pl. 24, figs. 15 a-c.

*Nonionella japonica* (Yokoyama). —Ujiié and Watanabe, 1960, p. 131, pl. 3, figs. 4a-c. —Kaiho, 1984b, p. 72, pl. 7, figs. 4a-c.

***Melonis affinis*** (Reuss) (Figure 11.5)

*Nonionina affinis* Reuss, 1851, p. 72, pl. 5, figs. 32a, b.

*Nonion aimonoi* Matsunaga, 1963, p. 109, pl. 37, figs. 2a, b.

*Melonis crassus* Kaiho, 1984a, p., pl. 2, figs. 6a, b, 129. —Kaiho, 1992b, p. 383, pl. 4, figs. 6a, b.

***Melonis pompilioides*** (Fichtel and Moll) (Figure 11.6)

*Nautilus pompilioides* Fichtel and Moll, 1798, p. 31, pl. 2, figs. a-c.

*Nonion pompilioides shimokinense* Asano, 1958, p. 71, pl. 13, figs. 14a, b.

*Melonis pompilioides* (Fichtel and Moll). —Kaiho, 1984b, p. 74, figs. 12a, b. —Kaiho, 1992b, p. 383, pl. 4, figs. 7a, b, pl. 6, figs. 5a, b.

**Remarks.**—Recent *Melonis pompilioides* lives in water deeper than the middle bathyal zone around Japan (Akimoto and Hasegawa, 1989). However, in the Poronai Formation, this species occurred in shallow marine fossil assemblages. The Paleogene *M. pompilioides* has a larger test than the Neogene specimens but in other biometrical aspects it fits the Recent *M. pompilioides* studied by Hasegawa (1983).

***Pullenia eocenica*** Cushman and Siegfus (Figure 11.7)

*Pullenia eocenica* Cushman and Siegfus, 1939, p. 31, pl. 7, figs. 1a, b. —Asano, 1958, pl. 11, figs. 13a, b.

*Pullenia* cf. *quinqueloba angusta* Cushman and Todd. —Fukuta, 1962, p. 25, pl. 8, figs. 4a, b.

*Pullenia compressiuscula* Reuss. —Ujiié and Watanabe, 1960, p. 131, pl. 3, Fig. 5.

**Remarks.**—This species is distinguished from *P. compressiuscula* and *P. quinqueloba angusta* in having a broadly rounded periphery and fewer chambers in the final whorl. All specimens examined in this study are replaced with pyrite.

***Pullenia salisburyi*** R. E. and K. C. Stewart (Figure 11.8)

*Pullenia salisburyi* R. E. and K. C. Stewart, 1930, p. 72, pl. 8, figs. 2a, b. —Asano, 1958, pl. 8, fig. 17. —Ujiié and Watanabe, 1960, p. 15, pl. 3, fig. 5. —Kaiho, 1984b, p. 72, pl. 7, figs. 7a,

b.

**Remarks.**—There are many records of this species around the North Pacific region, ranging in age from the Eocene to Recent. There has, however, been confusion among researchers on the relationship between *P. salisburyi* and *P. subcarinata* (d'Orbigny), which was originally described as *Nonionina subcarinata*. This study follows the views of the previous workers of the Japanese Paleogene.

***Heterolepa poronaiensis*** Kaiho (Figure 11.1)

*Heterolepa poronaiensis* Kaiho, 1984a, p. 128, pl. 11, figs. 5a-c, 7a-c.

***Criboelphidium ishikariense*** (Kaiho) (Figure 11.10)

*Elphidium ishikariense* Kaiho, 1984a, p. 125, pl. 10, figs. 2a, b.

**Remarks.**—This is the first record of this species from the Poronai Formation.

***Criboelphidium sorachiense*** (Asano) (Figure 11.9)

*Nonion sorachiense* Asano, 1954, p. 48, figs. 4a-5c.

*Elphidium sorachiense* (Asano). —Ujiié and Watanabe, 1960, p. 132, pl. 3, figs. 11, 12. —Kaiho, 1984b, p. 70, 71, pl. 6, figs. 12a, b.

***Criboelphidium wakkanabense*** (Kaiho) (Figure 12.1, 12.2)

*Elphidium asanoi* Kaiho, 1984a, p. 124, 125, pl. 10, figs. 1a, b. (non *E. asanoi* Matsunaga, 1963)

*Elphidium wakkanabense* Kaiho, 1992a, nom. nov. p. 143.

**Remarks.**—This species was originally described from the Wakkanabe Formation, Ishikari Group as *Elphidium asanoi*, and was first recorded from the Poronai Formation in the present study. *Elphidium wakkanabense* was proposed as a new name replacing *E. asanoi* Kaiho. The homonymic relationship with *E. asanoi* Matsunaga (1963) is still a primary one even though Matsunaga's species has features which cause me to remove it to the genus *Criboelphidium* based on my observation of Neogene specimens.

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## Appendix 1. Distributions of foraminifera in the

		*1 : Barren Foraminifera ; *2 : <i>Bulimina schwageri</i> - <i>Angulogerina hannai</i> ; *3 : Minaminaganuma Formation																	
well name		Numanohata SK-3D																	
Depth of Formation boundary (wireline depth in meter)		3649.0m								3804m									
Formation		*3 Poronai Formation								Ishikari Group									
Assemblage Zone		*1	*2	G. subgl.-C. sorachi.				E. subamakusaensis - H. crassiformis					*1						
Sample Depth (drilling depth in meter)		3640	3660	3680	3700	3720	3740	3760	3780	3800	3820	3840	3860	3880	3900	3920	3940	3960	3980
Ostracoda																			
AGGLUTINATED																			
<i>Bathysiphon</i>	<i>eocenica</i> Cushman and Hanna										1								
<i>?Ammodiscus</i>	sp. indet.																		1
<i>Glomospira</i>	sp.																		
<i>Cribrostomoides</i>	sp. cf. <i>C. cretacea</i> Cushman and Goudkoff																		
<i>Evolutinella</i>	<i>subamakusaensis</i> (Fukuta)								6						2				2
<i>Evolutinella</i>	sp. cf. <i>E. subamakusaensis</i> (Fukuta)											1							
<i>Haplophragmoides</i>	<i>crassiformis</i> Kaiho								2	3					1				1
<i>Haplophragmoides</i>	<i>rugosus soyaensis</i> Yasuda																		
<i>Haplophragmoides</i>	sp. cf. <i>H. rugosus soyaensis</i> Yasuda									1									
<i>Haplophragmoides</i>	<i>tanaii</i> Kaiho			2															
<i>Haplophragmoides</i>	sp. cf. <i>H. tanaii</i> Kaiho																		
<i>Haplophragmoides</i>	sp. A																		
<i>Haplophragmoides</i>	sp. B				4			1						2					
<i>Haplophragmoides</i>	sp. D										1	2	1						
<i>"Haplophragmoides"</i>	spp.			18	9	10	16	11	5	12	19	5	1	2	1			1	
<i>Budashevaella</i>	sp. aff. <i>B. multicamerata</i> (Voloshinova)																		
<i>Budashevaella</i>	<i>symmetrica</i> (Ujii and Watanabe)																		
<i>Budashevaella</i>	sp. cf. <i>B. symmetrica</i> (Ujii and Watanabe)																		3
<i>Budashevaella</i>	sp. indet.																		
<i>Recurvoidella</i>	sp. cf. <i>R. lamella</i> (Grzybowski)								1	13		5							
<i>Reticulophragmium</i>	<i>amakusaensis</i> (Fukuta)							2	2										
<i>Reticulophragmium</i>	sp. cf. <i>R. amakusaensis</i> (Fukuta)																		
<i>Cyclammina</i>	<i>ezoensis</i> Asano																		
<i>Cyclammina</i>	sp. cf. <i>C. ezoensis</i> Asano																		
<i>Cyclammina</i>	<i>pacifica</i> Beck		1			1		2		1					1				
<i>Cyclamminidae</i> genus et sp. indet.								3	9	1	4	1	7						
<i>Poronai</i>	<i>poronaiensis</i> (Asano)					1													
<i>Poronai</i>	sp. cf. <i>P. poronaiensis</i> (Asano)					1													
<i>Trochammina</i>	sp. cf. <i>T. asagaiensis</i> Asano			4	1			11											
<i>Trochamminidae</i> genus et sp. indet.				4	10	5		6											
Agglutinated miscellaneous			36	24	52		67	102	99	125	17	34	2	6					
PORCELLANEOUS																			
<i>Quinqueloculina</i>	<i>seminula compacta</i> Serova																		
<i>Quinqueloculina</i>	sp. indet.											1							
CALCAREOUS HYALINE																			
<i>?Dentalina</i>	spp.			1															
<i>Pseudonodosaria</i>	sp. cf. <i>P. conica</i> (Neugeboren)																		
<i>Pseudonodosaria</i>	sp. indet.																		
<i>Lagena</i>	sp. cf. <i>L. laevis</i> (Montagu)				1														
<i>Procerolagena</i>	sp. cf. <i>P. gracilima</i> (Seguenza)																		
<i>Guttulina</i>	<i>takayanagii</i> Kaiho																		
<i>Guttulina</i>	sp. cf. <i>G. takayanagii</i> Kaiho																		
<i>Pseudopolymorphina</i>	sp. A																		
<i>Sigmoidella</i>	<i>pacifica</i> Cushman and Oazwa																		
<i>Polymorphinidae</i> genus et sp. indet.								1	2	5	1								
<i>Fissurina</i>	sp. cf. <i>F. marginata</i> (Montagu)																		
<i>Glandulina</i>	<i>laevigata ovata</i> Cushman and Applin				1														
<i>Glandulina</i>	sp. indet.						2			1									
<i>Globocassidulina</i>	<i>globosa</i> (Hantken)			1	1	1		1											
<i>Globocassidulina</i>	spp.			1															
<i>Bulimina</i>	<i>schwageri</i> Yokoyama			1															
<i>Praeglobobulimina</i>	sp. cf. <i>P. ovata</i> (d'Orbigny)																		
<i>Praeglobobulimina</i>	<i>pyrula</i> d'Orbigny			2	1		1												
<i>Praeglobobulimina</i>	sp. indet.									1									
<i>Buliminidae</i> genus et sp. indet.																			
<i>Angulogerina</i>	<i>hannai</i> Beck																		
<i>Cibicides</i>	<i>elmaensis</i> Rau				2	1		1											
<i>Melonis</i>	<i>affinis</i> (Reuss)																		
<i>Melonis</i>	<i>pompilioides</i> (Fichtel and Moll)				1			2		3		1							
<i>Melonis</i>	sp. indet.						1												
<i>Pullenia</i>	<i>eocenica</i> Cushman and Siegfus									1									
<i>Pullenia</i>	<i>salisburyi</i> R.E. and K.C. Stewart																		
<i>Cribrorophidium</i>	<i>ishikariense</i> (Kaiho)									1									
<i>Cribrorophidium</i>	<i>sorachiense</i> (Asano)				17	3	15	6	20		13	8	5	2		2		1	
<i>Cribrorophidium</i>	sp. cf. <i>C. sorachiense</i> (Asano)									8									
<i>Cribrorophidium</i>	<i>wakkanabense</i> Kaiho					1			12	2		4							
<i>Cribrorophidium</i>	spp.				13	4	3		3	12	3	4		1		1			
Calcareous miscellaneous			4	2	1		10	13	13	15		7	2	3		1			
Percentage of Agglutinated Foraminifera		10	56	80	78	82	73	76	79	71	79	67	70	50	80	0	100		
Percentage of Porcellaneous Foraminifera		0	0	0	0	0	0	0	0	0	1.2	0	0	0	0	0	0		
Percentage of Calcareous Foraminifera		90	44	20	22	18	27	24	21	29	20	33	30	50	20	100	0		
Total population of Foraminifera		10	79	74	89	117	187	153	201	45	86	15	10	6	5	1	2		
Diversity (Species Richness)		4	4	10	5	5	5	3	7	3	4	3	0	2	2	1	1		
Diversity (Simpson's Index for Diversity)		3.6	1.7	7.4	1.6	2.7	2.5	3	3.5	1.5	3.6	2.8		1.8	1.8	1	1		

		Numanohata						
		3070.5m						
*3								
*1	<i>Bulimina schwageri</i> -A							
3060	3080	3100	3110	3120	3140			
						3		
					</			



**a SK-4D**

[illegible]

		*1 Barren foraminifera; *2 Minaminaganuma Formation																											
well name		KITA-AKEBONO SK-1D																											
Depth of Formation boundary (wireline depth in meter)		3067.0m																											
Formation		*2 Poronai Formation																											
Assemblage Zone		*1 Rare for aminifera Bulimina schwageri - Angulogerina hanna																											
Sample Depth (drilling depth in meter)		3060	3075	3080	3100	3120	3140	3150	3160	3170	3180	3190	3200	3210	3220	3230	3240	3250	3260	3270	3280	3290	3300	3310	3320				
Ostracoda	PLANKTONIC							1																					
Subbotina	sp. indet.																												
?PLANKTONIC miscellaneous																													
Bathysiphon	AGGLUTINATED																												
Bathysiphon	eocenica Cushman and Hanna												2	1															
Bathysiphon	vermoni Hamlin																												
?Bathysiphon	spp.											1	2	2															
Placentalmina	sp. A																								1				
Ammodiscus	spp.											1	1	1	2														
Glomospira	spp.															1													
Reophax	tappensis Asano																	3	1										
Reophax	sp. cf. R. tappensis Asano															1													
Reophax	sp.																			1									
Cribrostomoides	sp. cf. C. cretacea Cushman and Walters																												
Evolutinella	subamakusaensis (Fukuta)											1	8	26	6	2	24												
Evolutinella	sp. cf. E. subamakusaensis (Fukuta)																												
Haplophragmoides	crassiformis Kaiho																												
Haplophragmoides	sp. cf. H. crassiformis Kaiho											5	39	22	11	27	6	17											
Haplophragmoides	rugosus soyaensis Yasuda																												
Haplophragmoides	sp. cf. H. lanai Kaiho																												
Haplophragmoides	yokoyamai Kaiho																												
Haplophragmoides	sp. A																												
Haplophragmoides	sp. B																												
Haplophragmoides	sp. D																												
Haplophragmoides	spp.																												
Discamina	sp. indet.																												
Budashevaella	sp. aff. B. multicameratus (Voloshinova)																												
Budashevaella	symmetrica (Ujiei and Watanabe)																												
Recurviroides	sp. A																												
Recurviroides	spp.																												
Recurviroides	sp. cf. R. lemella (Grzybowski)																												
?Ammobaculites	spp.																												
*Clavulina *	sp. indet.																												
Alevallophragmium	spp.																												
Reticulophragmoides	amakusaensis (Fukuta)																												
Cyclammina	ezoensis Asano																												
Cyclammina	pacifica Beck																												
Cyclammina	sp. aff. C. pusilla Brady																												
Cyclamminidae genus et sp. indet.																													
?Dorothia	sp. indet.																												
Poronaiia	poronaiensis (Asano)																												
Trochammina	sp. cf. T. asagaiensis Asano																												
Trochammina	spp.																												
†fragment Clavulina like species's aperture end																													
Agglutinated miscellaneous																													
Quinqueloculina	PORCELLANEOUS																												
Quinqueloculina	seminula compacta Serova																												
Quinqueloculina	spp.																												
Miliolidae miscellaneous																													
Dentalina	CALCAREOUS HYALINE																												
*Dentalina *	sp. cf. D. suboboluta (Cushman) of Kaiho, 1984																												
Pseudonodosaria	spp. (fragments)																												
?Astacolus	conica (Neugeboren)																												
Lenticulina	sp.																												
Marginulina	sp.																												
Lagena	sp. cf. L. laevis (Montagu)																												
*Lagena *	spp.																												
Procerolagena	sp. cf. P. gracilima (Seguenza)																												
Guttulina	problema (d'Orbigny)																												
Guttulina	takayanagii Kaiho																												
Guttulina	sp. cf. G. takayanagii Kaiho																												
*Guttulina *	spp.																												
Pseudopolymorphina	hokkaidoana Kaiho																												
Sigmoidella	pacifica Cushman and Ozawa																												
Fissurina	sp. cf. F. marginata (Montagu)																												
Glandulina	laevigata ovata Cushman and Applin																												
Globocassidulina	globosa (Hantken)																												
Globocassidulina	spp.																												
Bulimina	schwageri Yokoyama																												
Praeglobobulimina	pyrula (d'Orbigny)																												
Globobulimina & Preglobobulimina spp.																													
Angulogerina	hannai Beck																												
Cibicides	sp. A																												
Cibicides	spp.																												
Notionella	japonica (Yokoyama)																												
Melonis	affinis (Reuss)																												
Melonis	pompilioides (Fichtel and Moll)																												
Pullenia	eocenica Cushman and Sieglus																												



[illegible]

## Appendix 3. Distributions of

		*1 : Barren Foraminifera ; *2 : Minaminaganuma Formation																												
well name		MITI Umaoi																												
Depth of Formation boundary (wireline depth in meter)		3640.0m																												
Formation		*2 Poronai Formation																												
Assemblage Zone		*1 <i>Bulimina schwageri</i> - <i>Angulogerina hannai</i>																												
Sample Depth (drilling depth in meter)		3620	3640	3660	3680	3700	3720	3740	3760	3780	3800	3820	3840	3860	3880	3900	3920	3940	3960	3980	4000	4020	4040	4060	4080	4100	4120			
Ostracoda																76	72	72										1		
PLANKTONIC																														
Planktonic foraminifera genus et sp. indet.																														
AGGLUTINATED																														
<i>Bathysiphon</i> <i>eocenica</i> Cushman and Hanna						1				1			3	5		1			5	2										
<i>?Ammodiscus</i> sp. indet.									1				1																	
<i>Glomospira</i> sp.																					1		1				2			
<i>Reophax</i> sp.																														
<i>Cribristomoides</i> sp. cf. <i>C. cretacea</i> Cushman and Goudkoff																	5													
<i>Evolutinella</i> <i>subamakusaensis</i> (Fukuta)			1	1							1		1	1	1											40	6			
<i>Evolutinella</i> sp. cf. <i>E. subamakusaensis</i> (Fukuta)																		4	3											
<i>Haplophragmoides</i> <i>rugosus soyaensis</i> Yasuda																														
<i>Haplophragmoides</i> sp. cf. <i>H. rugosus soyaensis</i> Yasuda																				2								3		
<i>Haplophragmoides</i> <i>crassiformis</i> Kaiho																					2	1	1							
<i>Haplophragmoides</i> sp. cf. <i>H. crassiformis</i> Kaiho							11	5				4	6																	
<i>Haplophragmoides</i> <i>tanaii</i> Kaiho																					3							6		
<i>Haplophragmoides</i> <i>yokoyamai</i> Kaiho														5	1					1										
<i>Haplophragmoides</i> sp. B																					1					1				
<i>Haplophragmoides</i> sp. D												1														3				
* <i>Haplophragmoides</i> spp.			6	6	3	12	8	5		24	7	3	14	32		40	17	25	3	10	10	7		3		10	11			
<i>Ammobaculites</i> sp. indet.																														
<i>Budashevaella</i> sp. aff. <i>B. multicamerata</i> (Voloshinova)										4				9			11			7										
<i>Budashevaella</i> <i>symmetrica</i> (Ujje and Watanabe)							2			1		3	6		2	7	4		2		15	1	2							
<i>Budashevaella</i> sp. indet.																					3									
<i>Recurviroides</i> sp. A										1						11	1													
<i>Recurviroides</i> sp. cf. <i>R. lamella</i> (Grzybowski)								5		2	2	4	4	1	14				2	3	2	10	2	9	2	4	32			
<i>Alveolophragmium</i> sp. A														2	1															
<i>Reticulophragmium</i> <i>amakusaensis</i> (Fukuta)																														
<i>Cyclammina</i> <i>ezoensis</i> Asano							2	2	1		2	1	2	11	4		5	9	8	1		4	6	10	10	8	2	1	2	2
<i>Cyclammina</i> <i>pacifica</i> Beck																														
<i>Cyclamminidae</i> genus et sp. indet.			1				6	3		14	11	9	4	23	6	10	8	8	11	12	6	5			2		4			
<i>Poronai</i> <i>poronaiensis</i> (Asano)							7	3		27	6	13	18	14	2	13	13	6	13	12	9	6	1	1	6	1	8			
<i>Trochammina</i> sp. cf. <i>T. asagaiensis</i> Asano																	5	2												
<i>Trochamminidae</i> genus et sp. indet.																						1	1							
* <i>Clavulina</i> sp. A														4	6															
<i>Clavulina</i> sp. indet.															1															
fragment of * <i>Clavulina</i> * like apertural end																1														
Agglutinated miscellaneous		16	4	21	26	39	47	21	77	30	40	56	107	30	153	74	25	32	73	109	71	18	15	8	40	101				
PORCELLANEOUS																														
<i>Quinqueloculina</i> sp. indet.										1						1														
CALCAREOUS HYALINE																														
<i>?Dentalina</i> spp.																	1		3		1									
<i>Lagena</i> <i>striata</i> (d'Orbigny)																				1										
<i>Lagena</i> sp. cf. <i>L. laevis</i> (Montagu)																														
<i>Guttulina</i> <i>takayanagii</i> Kaiho																														
<i>Guttulina</i> sp. cf. <i>G. problema</i> (d'Orbigny)							1													1										
<i>Pseudopolymorphina</i> sp. indet.																														
<i>Sigmoidella</i> <i>pacifica</i> Cushman and Oazwa																														
<i>Polymorphinidae</i> genus et sp. indet.																														
<i>Glandulina</i> <i>laevigata ovata</i> Cushman and Applin																														
<i>Glandulina</i> sp. indet.																									1					
<i>?Cassidulinoides</i> sp.																														
<i>Globocassidulina</i> <i>globosa</i> (Hantken)							1	2				1	6		2	1	2	1	2			1	2					1		
<i>Globocassidulina</i> sp.																														
<i>Bulimina</i> <i>schwageri</i> Yokoyama																														
<i>Globbulimina</i> sp. indet.																														
<i>Buliminidae</i> genus et sp. indet.																														
<i>Angulogerina</i> <i>hannai</i> Beck																														
<i>Nodogeneria</i> sp. cf. <i>N. lepidula</i> (Schwager)																														
* <i>Nonion</i> sp. indet.																														
<i>Nonionella</i> <i>japonica</i> Yokoyama																														
<i>Melonis</i> sp. cf. <i>M. affinis</i> (Reuss)																														
<i>Melonis</i> <i>pompilioides</i> (Fichtel and Moll)																														
<i>Melonis</i> sp. indet.																														
<i>Pullenia</i> <i>eocenica</i> Cushman and Sieglus																														
<i>Pullenia</i> <i>salisburyi</i> R.E. and K.C. Stewart																														
<i>Criboelphidium</i> <i>sorachiense</i> (Asano)																														
<i>Criboelphidium</i> spp.																														
Calcareous miscellaneous																														
Percentage of Agglutinated Foraminifera		100	54	53	72	100	94	81	69	73	66	86	87	40	60	99	81	42	52	75	92	89	97	79	95	83				
Percentage of Porcellaneous Foraminifera		0	0	0	0	0	0	0	0.4	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0				
Percentage of Calcareous Foraminifera		0	46	47	28	0	5.9	19	30	27	34	14	13	60	40	0.7	19	58	48	25	7.6	11	2.9	21	4.6	17				
Total population of Foraminifera		23	39	55	67	75	68	36	232	85	131	147	242	111	407	145	90	181	241	233	118	28	34	24	109	209				
Diversity (Species Richness)		2	6	6	6	4	6	4	12	8	11	10	14	10	13	9	10	11	12	14	11	7	4	7	7	12				
Diversity (Simpson's Index for Diversity)		1	1.8	2.1	1.9	2.3	3.6	2.7	3.9	3.5	2.9	6.8	5.7	1.7	2.7	5.5	5.2	2.9	3.6	5.6	4.8	5.3	2.1	5.3	1.4	4.3				



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# Feeding strategy of an Early Miocene cetothere from the Toyama and Akeyo Formations, central Japan

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**Abstract.** The feeding strategy of cetothere from the Toyama and Akeyo Formations is discussed based on the mandibles of two individuals. Three synapomorphic characters in the mandible that are shared with balaenopterid whales (a laterally projecting coronoid process, a marked inward elevation at the dorsal edge of the ramus posterior to the coronoid process, and a sharply edged ventral margin on the middle part of the mandible) suggest that some cetotheres had already acquired an engulfment feeding mechanism by the late Early Miocene. Two other apomorphic characters (a quite high and elongated dorsal mandibular ridge and a ventrally well-projected mandibular angle) suggest robust development of the musculature of the mandible during the feeding process in the studied specimens in contrast to the weak development of the musculature in the balaenopterids. This may represent a primitive transitional stage of the engulfment feeding mechanism which could be related to the lack or poor development of highly elastic elements in the ventral pouch.

**Key words:** Cetotheriidae, Early Miocene, engulfment feeding, feeding mechanism, mandible, Mysticeti

## Introduction

Mysticetes have acquired baleen plates and developed a unique filter feeding mechanism during the process of their evolution. The feeding strategy of the extant Mysticeti is generally divided into three types: skim feeding for plankton (Balaenidae), mud scooping (Eschrichtiidae), and engulfment feeding for fast-swimming krill and fish (Balaenopteridae) (Brodie, 1977; Pivorunas, 1979; Berta and Sumich, 1999). The evolution of filter feeding was a primary factor for the origin of mysticetes (Fordyce, 1980, 1989). Since the Cetotheriidae are the earliest true baleen-bearing, toothless mysticete family (Barnes, 1984; McLeod *et al.*, 1993; Fordyce and Barnes, 1994), the study of their feeding mechanism is important for considering the evolution of filter feeding in mysticetes. McLeod *et al.* (1993) pointed out that cetotheres have the following three morphological characteristics as compared with balaenopterids—(1) more posteriorly directed mandibular condyle; (2) larger coronoid process of mandible; and (3) longer zygomatic process of squamosal. Based on these characters, these authors briefly mentioned that cetotheres were probably engulfment feeders displaying a less specialized mandible and skull morphology and with a weaker throat groove than balaenopterids. However, there is no other detailed discussion in the literature about cetothere feeding

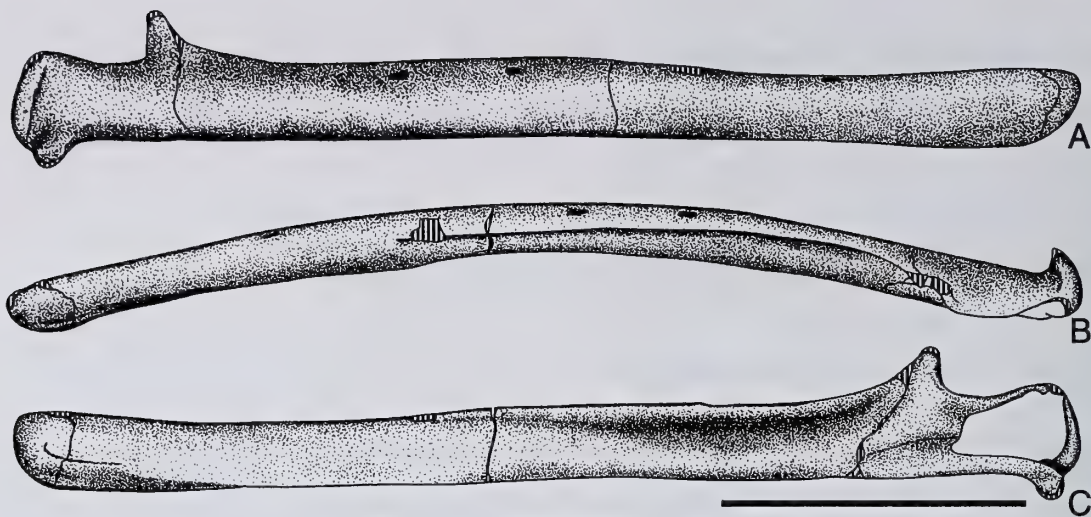
strategy.

Two cetothere mandibles were found from the Lower Miocene Toyama and Akeyo Formations, Gifu Prefecture, Japan. The mandible has a primary functional role for feeding, and its morphology may reflect to a high degree the feeding strategy. The purpose of this paper is to examine the feeding strategy of the cetotheres based on the two mandibles and to discuss the evolution of the engulfment feeding mechanism.

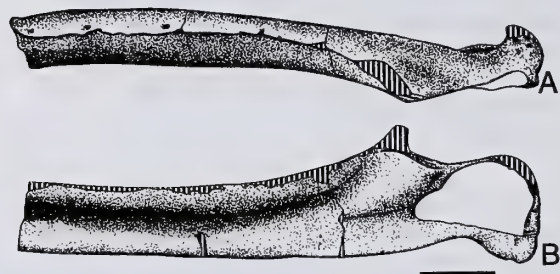
## Materials

Two cetothere specimens were examined in this study. Both specimens are deposited in the Mizunami Fossil Museum, Mizunami, Gifu Prefecture, Japan (MFM).

*MFM18124, Cetotheriidae gen. et sp. indet.* (Figure 1).—Both mandibles, skull fragments, cervical and thoracic vertebrae, ribs, a sternum, a humerus, and some bone fragments. The right mandible is almost complete. This specimen was found from the Kubohara Facies of the Toyama Formation, Iwamura Group, Iwamura town, Ena County, Gifu Prefecture, Japan (Kimura *et al.*, 2000). The horizon from which this specimen was collected is correlated to the Maki Member of the Toyama Formation, Iwamura Group (Ujihara *et al.*, 1992). The Maki Member is assigned to the *Crucidentacula sawamurae* Zone (late



**Figure 1.** Cetotheriidae gen. et sp. indet. from Toyama Formation, MFM18124, right mandible. A. Lateral view. B. Dorsal view. C. Medial view. Hachures indicate areas where mandible is damaged. Scale bar equals 50 cm. After Kimura *et al.* (2000).



**Figure 2.** Cetotheriidae gen. et sp. indet. from Akeyo Formation, MFM18125, right mandible. A. Dorsal view. B. Medial view. Hachures indicate areas where mandible is damaged. Scale bar equals 10 cm.

Early Miocene: Barron and Gladenkov, 1995; Yanagisawa and Akiba, 1998) based on diatom biostratigraphy (Ito *et al.*, 1999). This specimen was originally described by Kimura *et al.* (2000).

MFM18125, *Cetotheriidae* gen. et sp. indet. (Figure 2). —Right mandible. A posterior half of the mandible including condyle and angle is preserved. This specimen was found from the Lower Miocene Yamanouchi Member, Akeyo Formation, Mizunami Group, Togari, Mizunami City, Gifu Prefecture, Japan and was once referred to *Mysticeti*, gen. and sp. indet. (Kamei and Okazaki, 1974: p. 283, pl.97, figs.6a, b). The Akeyo Formation consists of the Tsukiyoshi, Togari, Yamanouchi, and Hazama Members in ascending stratigraphic order (Itoigawa, 1974, 1980). Kobayashi (1989) estimated the age of the Akeyo Formation to be 17–17.5 Ma on the basis of fission-track dating. Itoigawa and Sibata (1992) suggested that the

Yamanouchi Member is assigned to Upper Zone N.7 to Lower Zone N.8 of Blow (1969). Kohno (2000) also suggested that the Yamanouchi Member is late Early Miocene (ca. 18–17 Ma) based on the radiolarian and diatom dating.

These two mandibles share a characteristic morphology of a quite high and elongated dorsal ridge with a concavity at its medial side. This character clearly distinguishes the present species from any other known mysticetes. These edentulous specimens are clearly distinct from primitive, toothed mysticete families. Additionally, these two mandibles are characterized by the following combination of characters: (1) a large mandibular foramen; (2) a well-developed coronoid process that projects dorsally, laterally, and posteriorly; (3) a posteriorly directed articular surface of the condyle; (4) a sharply edged ventral margin on the middle part of the mandible. This combination of characters is not found in any extant mysticete families (*Balaenopteridae*, *Eschrichtiidae*, *Balaenidae*, and *Neobalaenidae*). Therefore, these two specimens are recognized as the same species in the *Cetotheriidae*, gen. and sp. indet. as will be discussed below (Kimura *et al.*, 2000). The *Cetotheriidae* have long been considered as a paraphyletic grade lacking the diagnostic characters of more derived mysticete families (e.g., Fordyce and Barnes, 1994).

For comparison, I examined the material of the following extant *Mysticeti* housed in the National Science Museum, Tokyo (NSMT): *Balaenopteridae*: *B. acutorostrata* (NSMT-M15941, NSMT-M32543), *B. edeni* (NSMT-M03538, NSMT-M32599); *Eschrichtiidae*: *E. robustus* (NSMT-M15940); *Balaenidae*: *B. glacialis* (NSMT-M03538).

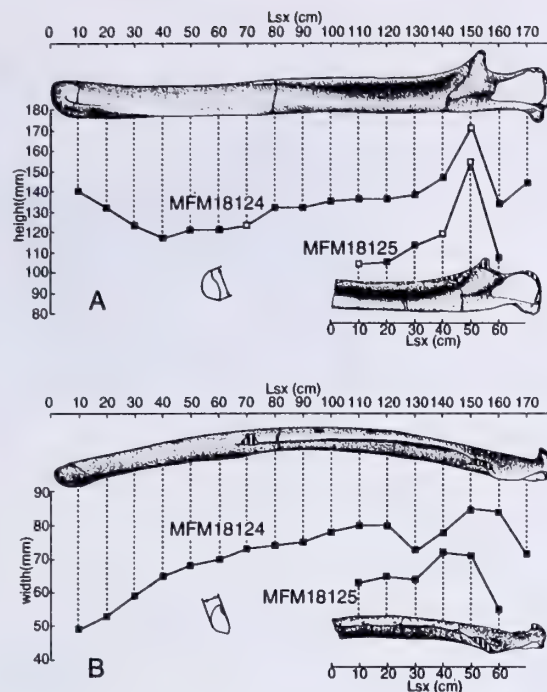


**Table 1.** Measurements of right mandible (in mm), Cetotheriidae gen. et sp. indet. from Toyama (MFM18124) and Akeyo (MFM18125) Formations.

	MFM18124	MFM18125		
Length of mandible in a straight line	1777	734+		
Length of mandible along outside curvature	1810	735+		
Distance from anterior end of ramus to level of center of coronoid process along outside curvature	1572	—		
Vertical diameter through coronoid process	214+	154+		
Vertical diameter of hinder end of ramus including condyle	187+	152+		
Transverse diameter of condyle	108+	80+		
Vertical (H) and transverse (W) diameter in 100-mm increments from the anterior end of ramus				
	H	W	H	W
100	140	49	104+	63
200	132	53	105	65
300	123	59	113	64
400	117	65	119+	72
500	121	68	154+	71
600	121	70	107	55
700	123+	73		
800	132	74		
900	132	75		
100	135	78		
1000	136	80		
1100	136	80		
1200	138	72		
1300	147	78		
1400	172+	85		
1500	133	84		
1600	145	71		
1700				

### Description

The right mandible of MFM18124 is almost complete except for erosion of an angle (an), a dorsolateral edge of a coronoid process (cp), and a dorsal and lateral part of a condyle (co) (Figure 1). All of the epiphyses on the preserved vertebrae (cervical and thoracic) are firmly ankylosed to the centra, and this condition in extant mysticetes is regarded as evidence of physical maturity (Omura, 1975). MFM18125 consists of only the posterior half of a right mandible and is smaller than MFM18124 by approximately 75% (Table 1). In MFM18125, the coronoid process is broken off except for its base and the dorsal and lateral portion of the condyle was eroded away (Figure 2). Unless otherwise mentioned, the descriptions



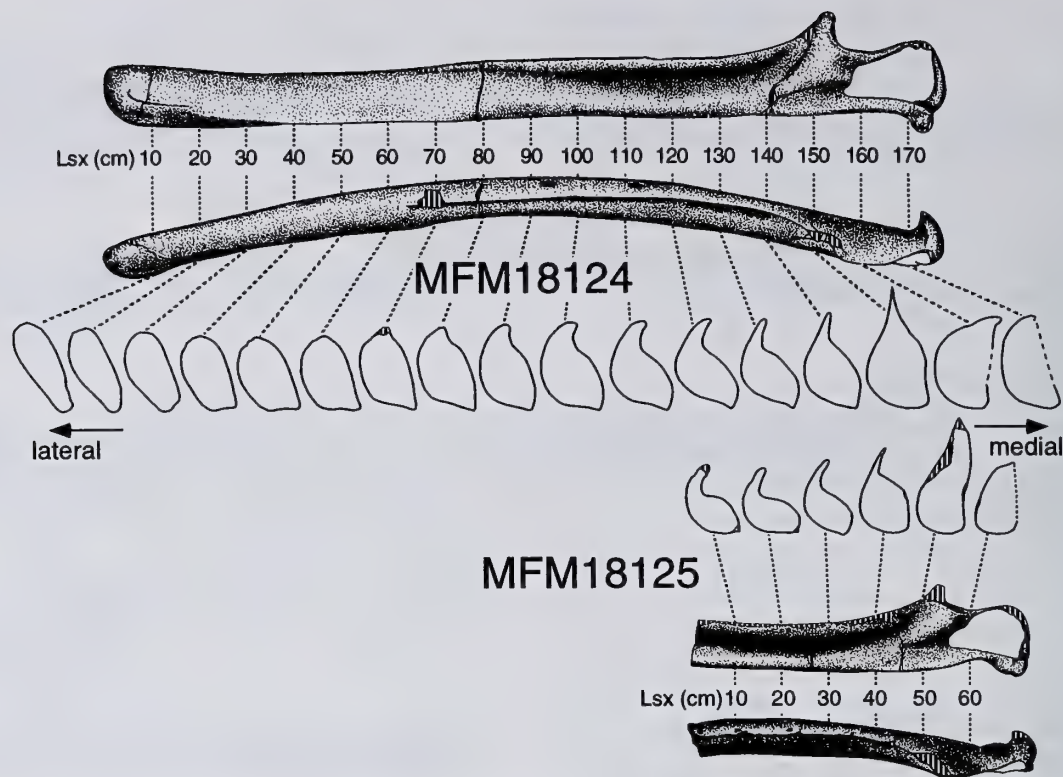
**Figure 3.** Change in measurements. A, B. Height (A) and width (B) of right mandible of MFM18124 and MFM18125 in 100-mm increments from anterior end, at left. Open squares represent minimum values, owing to breakage of specimen. Abbreviations: Lsx, distance between anterior end of ramus and measurement points along a straight line. Modified from Kimura *et al.* (2000).

are based on MFM18124.

A roughened area at the anterior tip of the mandible is short and does not exceed 75 mm. A longitudinal crease on the medial surface at the anterior tip of the mandible is 142 mm long. The horizontal ramus is rotated around its axis and its medial surface slopes lingually. The amount of rotation at the anterior tip of the horizontal ramus is about 30° against the medial surface at the region of the coronoid process. The horizontal ramus tapers slightly in dorsoventral diameter from the region of the coronoid process toward the anterior tip (Figure 3). However, the dorsoventral diameter increases at the anterior one-fifth of the mandible.

MFM18124 preserves three mental foramina along the dorsolateral surface of the mandible. These foramina occur at 485, 1010, and 1199 mm behind the anterior tip of the mandible and lie at 7, 31, and 43 mm below the dorsal margin of the horizontal ramus. These foramina open into an anteriorly directed groove.

Figure 4 shows the cross sections of the mandibles. There is a noticeable flattening of the anterior one-third of the medial surface of the mandible. Posterior to this, the medial surface of the ramus becomes convex medially. A concavity occurs at the medial side of the high dorsal ridge.



**Figure 4.** Cross sections of right mandible of MFM18124 (above) and MFM18125 (below). Hachures indicate areas where mandible is damaged. Dashed line in cross section represents mandibular foramen. Abbreviation: Lsx, distance between anterior end of ramus and measurement point along a straight line.

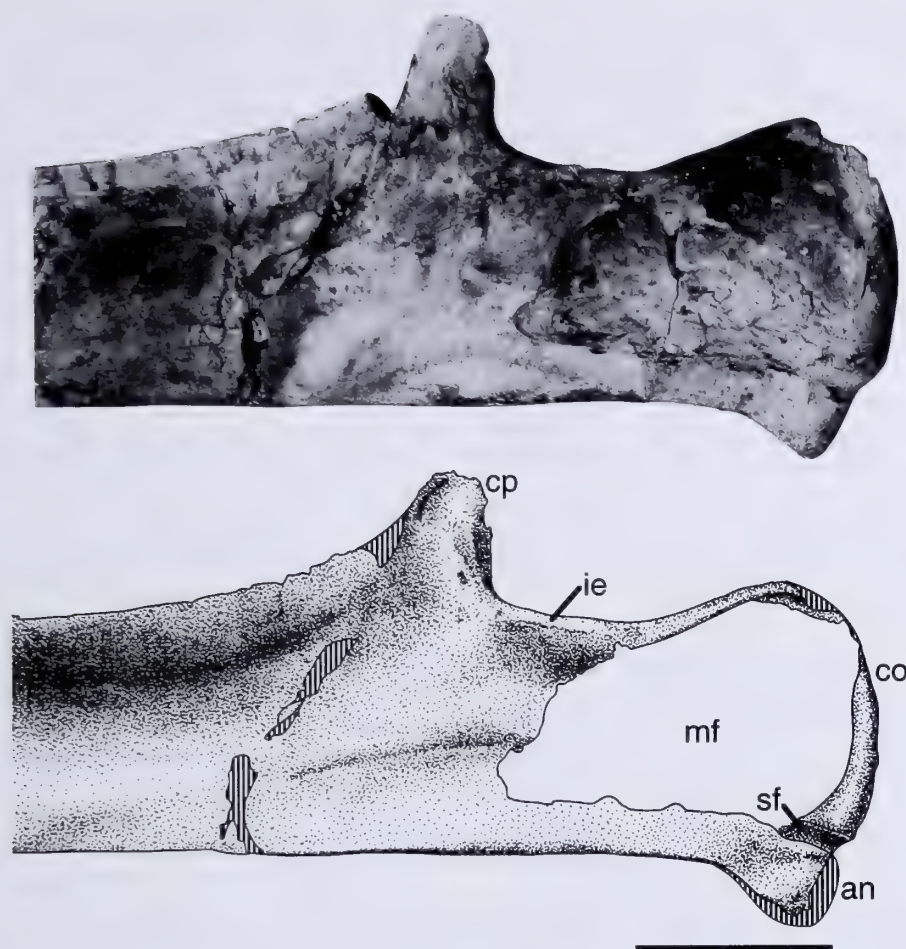
A groove is present on the medial surface of the horizontal ramus anterior to the mandibular foramen (mf). The lateral surface of the mandible becomes progressively convex dorsoventrally toward the posterior end. The greatest transverse diameter is below the midline at the middle part of the mandible. Further posteriorly, the greatest diameter shifts dorsally. Ventrally the lateral surface meets the medial surface to form a well-defined angular edge in the middle part of the mandible. This angular edge approaches the internal face anteriorly. The angular edge becomes rounded posteriorly at the region of the coronoid process.

In dorsal view, the mandible is only slightly bowed laterally (Figure 1B). The length of the mandible along the outside curvature represents only 102% of the length of the mandible in a straight line. The outward curvature is gradual and not abruptly flexed. There is no reflexion at the region of the coronoid process as in the balaenopterids. In lateral view, the ventral profile of the horizontal ramus is almost straight (Figure 1C). But in MFM18125, the ventral margin of the mandible anterior and posterior to the coronoid process is dorsally arched (Figure 2B).

The coronoid process projects dorsally, posteriorly, and laterally. The apex of the coronoid process is located at

87% of the length of the mandible along the outside curvature from the anterior extremity. The anterior margin of the coronoid process rises gradually, but its posterior margin descends abruptly. A shallow concavity occurs on the medial surface of the coronoid process along its anterior margin (Figure 5). Behind the apex, the posterior edge of the coronoid process thickens whereas the anterior edge remains thin. An inward elevation (ie) occurs on the medial surface of the upper border near the middle of the ramus behind the coronoid process (Figure 5). The inward elevation has a sharp edge and projects inward. It becomes more prominent anteriorly. This inward elevation continues anteriorly and dorsally to a ridge on the medial surface of the coronoid process. In MFM18125, because of breakage, a longitudinal groove occurs at a dorsomedial edge of the corresponding part of the ramus. But the remaining part projects slightly medially, and this suggests the development of the inward elevation in MFM18125. The inward elevation is also found in the Balaenopteridae. However, the elevation in the Balaenopteridae is more rounded than that of MFM18124 and MFM18125 (personal observation). For a distance of at least 880 mm anterior to the apex of the coronoid process, a relatively high dorsal





**Figure 5.** Cetotheriidae gen. et sp. indet. from Toyama Formation, MFM18124. A, B. photograph and drawing of posterior part of right mandible, medial view. Hachures indicate areas where mandible is damaged. Abbreviations: an, angle; co, condyle; cp, coronoid process; ie, inward elevation; mf, mandibular foramen; sf, subcondylar furrow. Scale bar equals 10 cm. Modified from Kimura *et al.* (2000).

ridge forms the dorsal edge of the horizontal ramus (Figures 1, 4). Anteriorly, the dorsal ridge becomes rounded and curved medially.

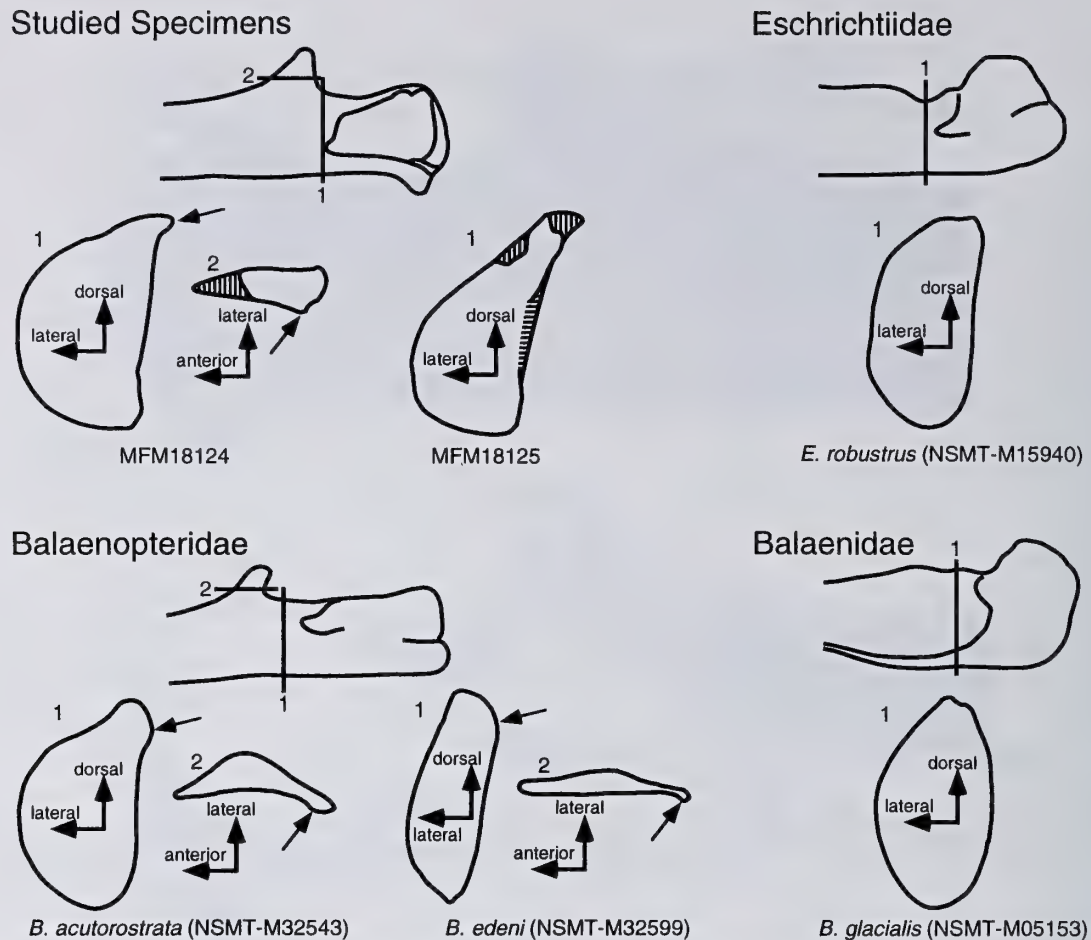
A mandibular foramen is large. The condyle is expanded from side to side and is more convex transversely than dorsoventrally. The forward-curving external border of the condyle projects beyond the lateral surface of the adjacent portion of the ramus. The maximum transverse expansion of the condyle (MFM18124, 108 mm+; MFM18125, 80 mm+) occurs below the midline of its vertical diameter. Ventrally, the condyle almost maintains its width. Ventrally, the condyle is bounded by a subcondylar furrow (sf) above the angle. This furrow extends across the posterior face of the condyle and decreases in depth laterally. Although the angle of MFM18124 is damaged, the preserved portion projects far ventrally. In MFM18125, the angle is almost complete, robust and projects ventrally (Figure 2).

## Discussion

Morphological characters of mysticetes can reflect their feeding strategy (McLeod *et al.*, 1993). Since the mandible plays an important role in feeding process, we can make inferences about the feeding strategy of fossil mysticetes from their mandibular morphology.

### Apomorphies for engulfment feeding

**Coronoid process.**—The coronoid process of the mandible in the balaenopterids is large and projects both posteriorly and laterally. The coronoid process in the basal suborder Archaeoceti and the toothed mysticetes Aetiocetidae is also large, but does not project laterally (Kellogg, 1936; Barnes *et al.*, 1995; Gingerich and Uhen, 1996; Hulbert *et al.*, 1998). The laterally projected coronoid process of the balaenopterids is considered to be a derived condition. In contrast, the non-engulfment feed-



**Figure 6.** Cross sections of mandible just behind (1) and base (2) of coronoid process (not to scale). Arrows indicate an inward elevation. Hachures indicate areas where mandible is damaged.

ers (Balaenidae, Neobalaenidae, and Eschrichtiidae) convergently acquired a quite small coronoid process (Barnes and McLeod, 1984) unless those three families form a monophyletic group.

The coronoid process provides the insertion for the temporal muscle which generates most of the elevating force during feeding in rorquals (Carte and MacAlister, 1868; Schulte, 1916; Lambertsen, 1983; Lambertsen *et al.*, 1995). The shape of the coronoid process is functionally important for engulfment feeding because it requires a complicated motion of the mandible (Lambertsen *et al.*, 1995). MFM18124 has a large and laterally projected coronoid process similar to the balaenopterids (Figures 1, 5). Although the coronoid process of MFM18125 is missing, the base of the process also suggests that the process is curved laterally (Figure 2B).

**Ventral margin of the mandible.**—The cross-sectional shape of the ventral margin of the middle part of the mandible is clearly differentiated among the mysticete families (Deméré, 1986; Nagasawa, 1994). In the Balaenopteridae,

the ventral margin of the cross section in the middle part of the mandible forms a well-defined angular edge (Deméré, 1986; Kimura *et al.*, 1987; Nagasawa, 1994). The sharply edged ventral margin of the cross section in the middle part of the mandible is also developed in MFM18124 and MFM18125. The mylohyoid muscle is attached along this ventral ridge (Pivorunas, 1977; Lambertsen, 1983). In engulfment feeding, the mylohyoid muscle, together with other muscles (multiple muscle layers: Lambertsen, 1983), plays an important role in expelling the sea water through the baleen plates (Lambertsen, 1983; Orton and Brodie, 1987). The marked ridge on the ventral margin of the mandible suggests the presence of well-developed mylohyoid muscles.

**Inward elevation of the mandible.**—The degree of development of the elevation is variable in the Balaenopteridae, stronger in *B. acutorostrata* than in *B. edeni* (Figure 6). This inward elevation is also found in *B. musculus* (Struthers, 1889). In *Megaptera novaeangliae*, the elevation rises upward on the same part of the mandible and



is called the post-coronoid elevation (Struthers, 1889). The studied specimens have a remarkable inward elevation on the medial surface of the upper border near the middle of the ramus behind the coronoid process similar to the balaenopterids.

In contrast, the structure of the corresponding part is quite different in the Eschrichtiidae and Balaenidae. In the Eschrichtiidae, the coronoid process is quite low and projects laterally. Posterior to the coronoid process, there is a low process which projects dorsally, and this process continues posteriorly to a low ridge on the medial surface of the ramus. Below this low ridge, another longitudinal faint ridge is also present. In the Balaenidae (*B. glacialis*), the coronoid process is faint and, posterior to the coronoid process, a shallow groove is present on the dorsomedial surface of the ramus (anteroposterior length of the groove: right 46 mm/left 59 mm). This groove makes a low bump on the medial surface of the upper part of the ramus. Although there is a ridge on the dorsomedial surface of the ramus in both families, the ridge is faint and does not project medially (Figure 6). Further, there is no ridge on the medial surface of their quite low coronoid process. Therefore, these structures found in the Eschrichtiidae and Balaenidae are clearly distinguished from the prominent inward elevation present in the studied species and the Balaenopteridae.

The frontomandibular stay is a functionally and anatomically specialized tendon of the temporal muscle and is attached to the inward elevation (Struthers, 1889; Lambertsen *et al.*, 1995). This stay apparatus is common among the balaenopterids and serves to support the motion of the mandible during the feeding process, especially in initiating engulfment (Lambertsen *et al.*, 1995).

The above three characters suggest that the species had an acquired engulfment feeding mechanism. The Cetotheriidae is believed to include taxa closely related to the ancestor of the Balaenopteridae (Fordyce and Barnes, 1994). The three apomorphies are also found in the Balaenopteridae. However the phylogenetic relationship between the cetothere species in this study and the Balaenopteridae is still unclear and the analysis of the relationship is beyond the scope of this study. So, more detailed consideration is needed to ascertain whether these characters are synapomorphies between the two.

### Efficiency of engulfment feeding

One aspect of engulfment feeding efficiency relates to the size of the mouth cavity. The mandible of the studied specimens is slightly curved, a primitive condition (Barnes and McLeod, 1984). Deméré (1986) suggested that the width of the rostrum is directly proportional to the extent of the lateral curvature of the mandible. This suggests that the mouth cavity of the studied specimens was relatively

small and that engulfment feeding in MFM18124 and MFM18125 was less efficient than in the extant balaenopterids.

The mandible of the balaenopterids changes continuously in its position during the engulfment feeding process by three motions—(1) alpha rotation: an inward and outward rotation around the longitudinal axis of the mandible; (2) delta rotation: depression and elevation of the mandible; and (3) omega rotation: medial and lateral movement of a condyle of the mandible (Lambertsen *et al.*, 1995). The temporomandibular articulation in extant balaenopterids is, unlike other mammals, composed of a fibrous meniscus infiltrated with oil (Hunter, 1787; Carte and MacAlister, 1868; Beauregard, 1882; Beneden, 1882; Struthers, 1889; Schulte, 1916). Since this meniscus enables the movement of articulation more effectively, like planar quadrilateral connecting system, the squamomandibular articulation of the balaenopterids can perform its complicated movements (Lambertsen *et al.*, 1995). Cetotheres are generally characterized by having a more or less flattened articular surface of the squamosal (Miller, 1923). This suggests that the temporomandibular articulation composed of a fibrous meniscus was not acquired or poorly developed in the Cetotheriidae. Neither of the studied specimens includes the squamosal, and it is unclear that they were able to perform these complicated movements of the mandible.

Lambertsen *et al.* (1995) suggested that stronger lateral curvature and elongation of the mandible would increase alpha-rotation of the mandible. If these specimens were able to perform alpha-rotation, the small amount of curvature suggests that this could not contribute greatly to the enlargements of the mouth. This suggests that cetotheres fed less efficiently than the balaenopterids.

### Feeding strategy of Balaenopteridae

In the Balaenopteridae, the musculature of the mandible mainly braces the jaw during engulfment feeding and does not actively open it (Lambertsen, 1983; Orton and Brodie, 1987; Lambertsen *et al.*, 1995). This passive movement of the mandible is mainly caused by water pressure resulting from locomotion and allied action of a ventral pouch (Brodie, 1977; Orton and Brodie, 1987; Lambertsen *et al.*, 1995; Bakker *et al.*, 1997). The ventral pouch (body wall below the cavum ventrale: Lambertsen, 1983) is a highly elastic grooved structure which consists mainly of blubber and multiple muscle layers, covering the ventral surface of the whale from the anterior border of the mandible to the umbilicus or further (Pivorunas, 1979; Lambertsen, 1983; Orton and Brodie, 1987). The pouch is filled by voluntary increase of the curvature of its elastic ventral wall by contraction of multiple muscle layers. This changes the water flow between the upper and lower surface of the head and causes asymmetry of the hydraulic pressure which assists in



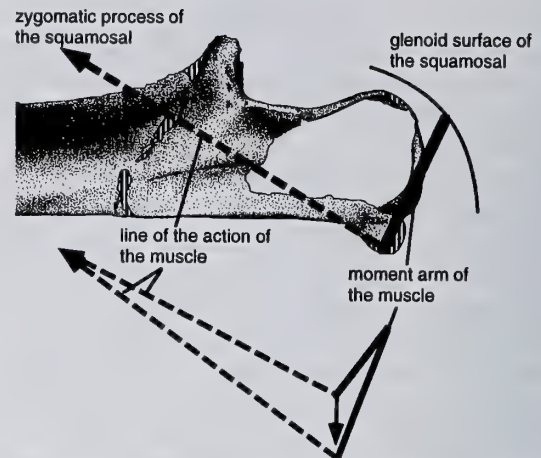
depressing the mandible (Bernoulli principle) (Lambertsen *et al.*, 1995). The passive movement of the mandible in filling the pouch is also suggested by the fact that the relaxation of jaw musculature makes the lower jaw drop (Lambertsen, 1983). Lambertsen *et al.* (1995) also suggested that as a result of the mode of attachment of the ventral pouch to the mandible, hydraulic pressure can rotate the mandible around its longitudinal axis (alpha rotation). Active contraction of musculature is required for water expulsion, especially in the final phase (Lambertsen, 1983; Orton and Brodie, 1987). Orton and Brodie (1987) suggested two sources for passive motion of the mandible in expulsion and these are accompanied with changes in swimming speed. They are based on a recoil of hydraulic pressure and resiliency of elastic elements of the ventral pouch. In addition, when the whale ceases propulsive action, the energy of the frontomandibular stay against the water flow is released and the stored energy of the stay assists closure of the mouth (Lambertsen *et al.*, 1995).

Therefore, we can summarize the source for the efficient feeding mechanism of the Balaenopteridae as follows: (1) the strong development of the highly elastic elements in the ventral pouch; (2) the multiple muscle layers which serve to deepen the oral cavity; (3) the frontomandibular stay.

#### Feeding strategy of studied specimens

The specimens studied display the aforementioned synapomorphies with the balaenopterids, but also show two apomorphic characters, which are clearly different from the Balaenopteridae. Both these characters suggest that engulfing is a more active muscular process than in the Balaenopteridae.

**Dorsal ridge.**—The specimens studied have a relatively high and elongated dorsal ridge with a concavity at its medial side (Figures 1, 2, 4). In MFM18124, there is a roughened area on most of the medial surface of the ridge. This area can be considered as the origin of the caudal part of the mylohyoid muscle. The mylohyoid muscle is only attached along the ventral border in the extant Mysticeti (*B. acutorostrata*: Pivorunas, 1977, Lambertsen, 1983; *B. borealis*: Schulte, 1916) and the extant Odontoceti (Reidenberg and Laitman, 1994) at the middle part of the mandible. But in ungulates, the muscle is separated into rostral and caudal parts, and the caudal part originates from the medial surface of the mandible just ventral to the alveolar border (Getty, 1975; Sisson, 1975; Nickel *et al.*, 1986). The close relationship between cetaceans and ungulates has been confirmed by much paleontological and molecular data (e.g., Van Valen, 1966; Shimamura *et al.*, 1997). It appears that cetotheres display the primitive ungulate muscle pattern; the dorsal ridge and allied concavity may indicate the area for the attachment of the mylohyoid muscle. Therefore,



**Figure 7.** Schematic diagram showing moment arm of superficial portion of masseter muscle (above) and changing of moment arm caused by ventral projection of angle (below). Solid and dashed lines indicate moment arm of muscle and line of action of muscle, respectively.

the relatively high dorsal ridge with the well-developed concavity of the specimens studied suggests a highly developed mylohyoid muscle, unlike the balaenopterids.

The mylohyoid muscle is the largest muscle in the multiple muscle layers of the floor of the mouth. The multiple muscle layers of the ventral pouch are the primary contributor for active expulsion of water through the baleen (Lambertsen, 1983). In addition, at the final phase of water expulsion, the tongue is forced upwards by contraction of the mylohyoid muscle and this forcibly expels the remaining sea water through the baleen (Lambertsen, 1983). The mylohyoid muscle is primarily an elevator of the tongue (Yamaoka *et al.*, 1992). Thus, the development of the mylohyoid muscle suggests that the studied specimens required active musculature for water expulsion during feeding.

**Angle.**—The angle provides the insertion of the muscles for the movement of the mandibles, such as the medial pterygoid muscle, the digastricus muscle, and the superficial portion of the masseter muscle (Carte and MacAlister, 1868; Schulte, 1916; Lambertsen *et al.*, 1995). The angle of the specimens studied is large and projects ventrally (Figure 1, 2). This is clearly shown by the ratio of mandibular height through angle to mandibular length along outside curvature of the adult individual (converted to percentages): MFM18124 10.3+%; *B. acutorostrata* 8.5–9.5% (Turner, 1891–1892; Omura, 1975), *B. edeni* 7.9–9.2% (Omura *et al.*, 1981), *B. musculus* 8.3–9.3% (Struthers, 1889; Omura *et al.*, 1970), *B. borealis* 7.6–8.1% (Nishiwaki and Kasuya, 1971), *M. novaeangliae* 9.1% (Struthers, 1889). The ventrally projected angle implies that the area for the insertion of the muscle is also posi-



tioned ventrally. This would increase the moment arm of the superficial masseter and thus improve the mechanical advantage of the mandible (Herring and Herring, 1974; Vizcaíno and Bargo, 1998) (Figure 7). Therefore, the morphology of the angle suggests that the specimens studied could produce a more powerful motion of the mandible compared with the balaenopterids.

Both of these characters suggest the active contribution of the musculature of the mandible during feeding. This is in marked contrast to the passive contribution of the musculature of the mandible in the Balaenopteridae. The sources for the efficient feeding mechanism in the Balaenopteridae have been summarized above. In the specimens studied, the sharply edged ventral margin at the middle part of the mandible and the well-developed inward elevation indicates the development of the mylohyoid muscle and therefore the multiple muscle layers and frontomandibular stay, respectively. Therefore the robust contribution of the musculature of the specimens studied can be explained by the lack or poor development of the highly elastic elements in the ventral pouch.

### Conclusion

I propose the following scenario of evolution of the engulfment feeding mechanism in baleen whales. Early mysticetes (aetiocetids) used filter feeding with teeth, and later cetotheres used baleen. Engulfment feeding was present in Cetotheriidae by the late Early Miocene. However, the feeding mechanism in the Early Miocene cetotheres required more active musculature than in the balaenopterids because of poor development or lack of the highly elastic elements in the ventral pouch. The well developed elastic elements in the skin are highly characteristic and are one of the key structures enabling passive movement of the mandible in the Balaenopteridae. The elastic elements evolved in the Balaenopteridae and enhanced efficiency of the mandible. In addition, balaenopterids have lost the apomorphic characters unrelated to the active musculature of the mandible during engulfment feeding. The feeding strategy suggested by the studied specimens may represent a primitive transitional stage of the evolution of the engulfment feeding mechanism.

The skull morphology may also exert an influence on the feeding mechanism (McLeod *et al.*, 1993). However, no skull was preserved in both specimens studied, except for a few fragments of the skull in MFM18124. Generally, cetotheres are characterized by primitive skull morphology. The apomorphic characters of the specimens studied which suggests more active contribution of the musculature of the mandible during the feeding process might not only be due to its feeding mechanism, but also to its primitive skull morphology. An additional specimen with a well-

preserved skull is needed to address the feeding strategy of the studied specimens in more detail.

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# Ostracodes from the Inter-trappean beds (Early Paleocene) of the east coast of India

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**Abstract.** Twenty-seven ostracode species from the Inter-trappean beds (Paleocene) of Duddukuru, West Godavari District, Andhra Pradesh, east coast of India are recorded and/or described. Nine species—*Cytheromorpha godavariensis*, *Cytherura duddukuruensis*, *Hapsicytheridea undulata*, *Krithe bhandarii*, *Paracandona andhraensis*, *Munseyella indica*, *Neomonoceratina paraoertlii*, *Semicytherura diluta*, and *Uroleberis rasilis*—are new. The identification of 6 species, previously described from the east coast of India, and also recorded in this work, are revised. The stratigraphic distribution, age and affinity and paleoecology of the ostracode fauna are also discussed.

**Key words:** Duddukuru, East Coast of India, Inter-trappean beds, Ostracodes, Paleocene

## Introduction

The Inter-trappean beds of the east coast of India are a key marker horizon in the stratigraphy of the country. They are of great significance in fixing the age limits of the Deccan Traps, at least those of this part of the peninsula, with which these beds are closely associated. This is because of their unique stratigraphic position (Table 1) and the prolific marine microfauna they contain. There are, however, varied opinions about the age of the Inter-trappean beds and vis à vis of the associated Deccan Traps. Most of the earlier workers until the nineteen seventies considered the Inter-trappean beds as Tertiary in age, ranging from Paleocene to Eocene (Hislop in Hislop *et al.*, 1860; Sahni, 1934; Rao and Rao, 1935, 1937a, 1937b; Rao *et al.*, 1936; Rao, 1956; Sastri, 1961; Bhalla, 1967). However, these views changed markedly in the nineteen eighties during which the Deccan volcanism was demonstrated to be a major Cretaceous-Tertiary boundary (KTB) event (Courtillet *et al.*, 1986, 1988, 1990; Bakshi, 1987; Duncan and Pyle, 1988; Hallam, 1988; Sahni and Bajpai, 1988). Govindan (1981) using foraminifera from the Inter-trappean sediments from Narsapur-1 well section from Krishna-Godavari (KG) Basin (of which the present area of Duddukuru under study is a part) assigned the Deccan Traps of this well to late Maastrichtian, emplaced between 70–67 Ma. Subsequently, Raju *et al.* (1991, 1994, 1995), Jaiprakash *et al.* (1993), Saxena and Mishra (1994), and Mishra *et al.* (1994) studied foraminifera, calcareous nannoplankton and dinoflagellate cysts from more

well sections from the K-G Basin. The data suggest that the volcanism began during 65.5 to 65 Ma (considering KTB at 65 Ma, Sharpton *et al.*, 1992) in the terminal Cretaceous and continued across the KTB into the early Paleocene.

The microfauna of the Inter-trappean beds of the east coast of India comprises mainly foraminifers and ostracodes. A survey of the literatures reveals that important contributions on these foraminifers have been made by Rao and Rao (1937a), Sastri (1961), Bhalla (1967), Govindan (1981), Raju and Dave (1993), and Jaiprakash *et al.* (1993), while on ostracodes by Jain (1978) and Bhandari (1995).

With the intention of working on the ostracode fauna of the Inter-trappean beds of the east coast of India the authors collected samples of these beds from two sections. The location of the sections is given below and also in Figure 1.

Section I is from a limestone quarry, belonging to M/S Facor Ltd., about 1 km south of the village of Duddukuru (17° 2' 15" N; 81° 35' 30" E) on the Eluru-Kovvur Road, West Godavari District, Andhra Pradesh, east coast of India. Section II is from an abandoned quarry about 2 km southeast of Duddukuru. Both sections yielded a prolific, well preserved ostracode fauna much richer than those reported by Jain (1978) and Bhandari (1995). The assemblage comprises a total of 27 species including 9 new ones and a number of species being reported for the first time from the region. This has necessitated revising the ostracode fauna of the Inter-trappean beds of the east coast of India. A new genus *Costabuntonia* has recently been

proposed for the species previously described as *Protobuntonia hartmanni* Jain (Khosla, 1999).

### Previous work

Among the earlier works on the ostracode fauna from the Inter-trappean beds of the east coast of India, an important contribution was made by Sastri (1961 and 1963) who reported the occurrence of nine species from these beds at Kuntamuru village near Rajahmundry. These species are *Cytherella* sp., *Cytheropteron* sp., *?Eucythere* sp., *Loxoconcha* sp., *Bairdia subdeltoidea* (Münster), *Cythere* (*?Xestoleberis*) *ranikotiana* Latham, *Cythereis bowerbanki* Jones, *Cythereis* cf. *mersondaviesi* Latham, and *Cytherelloidea* sp. Of these only the last five species were described and illustrated in his 1963 paper while the specific name *Cythere* (*?Xestoleberis*) *ranikotiana* was modified as *Cythere ranikotiana*. Bhalla (1965) recognised 16 ostracode species from Pangadi, Andhra Pradesh. These are: *Brachycythere* sp., *Bythocypris* sp., *Costa* sp., *Cytherella* sp., *Cytheretta* [possibly *C. laticostata* (Reuss)], *Hermanites* sp. A, *H.* sp. B, *Krithe* [provisionally identified as *K. bartonensis* (Jones)], *Leguminocythereis* sp. A, *L.* sp. B, *Neocyprideis* sp., *Occultocythereis* sp., *Quadracythere* sp., *?Schizocythere* sp., *Semicytherura* [provisionally identified as *S. forestensis* (Keij)], and *Xestoleberis* [provisionally identified as *X. subglobosa* (Bosquet)]. Their stratigraphic distribution and paleoecologic significance were given in his subsequent paper (Bhalla, 1967). Bhalla (1979a–c, 1980) described and illustrated the following new species from the Pangadi area: *Hermanites sastryi*, *Loxoconcha singhi*, *Occultocythereis elongatum*, and *Quadracythere tewarii*.

Guha (1970) recorded *Cythereis* cf. *tamulicus*, *Hermanites* cf. *pondicheriensis*, *Paracypris* sp., *Protobuntonia* sp., *Xestoleberis* sp., and the genus *Ovocysteridea*.

Jain (1978) described and illustrated twelve ostracode species from Kateru, Rajahmundry. Of these two species, *Ovocysteridea raoi* and *Protobuntonia hartmanni* are new, the other species represented being "*Bairdia*" sp. indet., *?Bythocypris* sp. indet., *Cytherella* sp. cf. *münsteri* (Roemer), *Cytherelloidea* sp. cf. *C. keiji* McKenzie, *?Cytheridea* sp. indet., *Hermanites* sp. cf. *H. cracens* Siddiqui, *Limnocythere* sp. indet., *Loxoconcha* sp. indet., *Quadracythere* (*Hornibrookella*) *subquadrata* Siddiqui, and *?Xestoleberis* sp. indet.

Bhandari (1995) recorded 15 species from the Inter-trappean beds near Duddukuru, Andhra Pradesh. Of these four species—*Cushmanidea bhatiai*, *Cytherella mohani*, *Cytheridella rajahmundryensis* and *Palmoconcha rajui* are new. The other species reported are *Bythocypris*? sp., *Cytherelloidea* sp. cf. *C. keiji* McKenzie, *Cytheridella* sp., *Gyrocythere* sp. cf. *G. parvicarinata* Siddiqui, *Hermanites*

*sastryi* Bhalla, *Hermanites* sp., *Hornibrookella tewarii* (Bhalla), *Nucleolina diluta* Al-Furaih, *Ovocysteridea raoi* Jain, *Protobuntonia hartmanni* Jain, and *Xestoleberis* sp.

### Stratigraphy

The geology of the region, along with a detailed map, has been adequately described by Bhalla (1967) and this has been followed in this work. The Inter-trappean beds are set of sedimentary strata composed mainly of limestone with shale/claystone intercalations lying in between the Deccan trap. The generalised stratigraphy of the coastal tract of the Krishna-Godavari districts, Andhra Pradesh is summarised in Table 1 (for details see references in Ramam and Murty, 1997).

The Intra-trappean beds have a gentle dip of 4 to 6 degrees towards the southeast and thickness varying from less than a meter to a little over 9 meters. The samples from which the present ostracode fauna was obtained come from the two sections. The sequence of these sections is given in Tables 2 and 3.

### Materials and methods

The samples were broken into small pieces and boiled for 3–4 hours in water to which one or two tablespoons of soda ash were added. The disintegrated material was wet screened through set of sieves of 30, 80, and 150 mesh size. The dried, washed residue was uniformly spread on a picking tray and scanned under a stereozoom microscope. The ostracodes present were hand picked with a fine sable-hair brush and arranged in assemblage slides. The type specimens were photographed on Jeol SEM using ORWO 120, black and white 100 ASA film. A total of 4,040 ostracodes were picked up, counting both complete carapaces and open valves as individual specimens. Their distribution is given in Table 4 and all the species recognized in this work are illustrated in Figures 2–5.

### Composition, age and affinity of ostracode fauna

The ostracode fauna of the Inter-trappean beds of Duddukuru comprises 27 species (Table 1). These belong to 13 families, 4 species each to the families Cytherellidae, Cytheridae, and Cytheruridae, 3 species each to the families Hemicytheridae and Trachyleberididae, two species to the family Xestoleberididae, and one species each to the families Bairdiidae, Candonidae, Cushmanidae, Cytherideidae, Krithidae, Limnocythereidae and Loxoconchidae. An analysis of these is given below.

1. Three species are left under open nomenclature and nine species are considered new. These are of little use in age interpretation at present.



**Table 1.** Generalized stratigraphy of the coastal tract of the Krishna-Godavari districts, Andhra Pradesh.

Age	Formation
Quaternary	Alluvium
Mio-Pliocene	Rajahmundry Formation
Late Maastrichtian-Early Paleocene	Deccan Trap with Inter-trappean beds
Late Maastrichtian	Infra-trappean Limestone
Late Cretaceous	Tirupati Formation
Early Cretaceous	Raghavapuram Formation
Triassic-Jurassic	Kota Formation (Upper Gondwana)
Permian	Kamthi Formation (Lower Gondwana)
Archean	Khondalite

**Table 2.** Stratigraphic succession of Section I.

Sample No.	Lithology	Thickness in meters
	Black colored basalt	1.2
	Grey shale	0.45
	Red shale	0.45
I/10-11	Light yellow limestone	2
I/9	Yellowish grey clay	0.15
I/8	Light yellow limestone	0.76
I/6-7	Yellowish grey clay	0.25
I/4-5	Brownish yellow marl	0.3
I/3	Grey clay	0.3
I/2	Greyish white clay	0.25
I/1	Light yellow limestone	2.44
	Black colored basalt	Base not exposed

**Table 3.** Stratigraphic succession of Section II.

Sample No.	Lithology	Thickness in meters
II/6-8	Greyish white limestone	0.81
II/5	Grey clay	0.38
II/1-4	Light yellow limestone	1.22
		Base not exposed

2. Eight species, *Costabuntonia hartmanni* (Jain), *Cushmanidea bhatiai* Bhandari, *Cytherella mohani* Bhandari, *Falsocythere elongata* (Bhalla), *Hermanites sastryi* Bhalla, *Hornibrookella tewarii* (Bhalla), *Neocyprideis raoi* (Jain), and *Palmoconcha rajui* Bhandari, have so far been known only from Duddukuru (Jain, 1978; Bhalla, 1979b, c, 1980; Bhandari, 1995).

3. One species, *Xestoleberis subglobosa* (Bosquet), has been recorded widely from the Eocene beds of France, Belgium, Netherlands (Keij, 1957) and also from the Middle Eocene of Kachchh, western India (Guha, 1968; Khosla and Pant, 1988), Himachel Pradesh, northern India (Mathur, 1969) and the Lower Eocene of Rajasthan, western India (Khosla, 1972).

4. One species, *Bairdia beraguaensis* Singh and Tewari, has previously been recorded from the Early Eocene beds

of Jammu and Kashmir (Tewari and Singh, 1966), Pakistan (Sohn, 1970), Rajasthan (Khosla, 1972), Meghalaya (Singh, 1984) and from the Middle Eocene beds of Assam (Neale and Singh, 1985).

5. Three species, *Cytherelloidea bhatiai* Guha and Shukla, *Paijenborchellina indica* (Khosla) and *Paracypris khuialaensis* Bhandari, have been described from the Early Eocene beds, the first from Vridhachalam, Tamilnadu, southern India (Guha and Shukla, 1974), the other two from Rajasthan (Khosla, 1972; and Bhandari, 1996). *P. indica* has also been reported from Kachchh (Khosla and Pant, 1988).

6. Two species, *Holcopocythere bassiporosa* Al-Furaih and *Nucleolina diluta* Al-Furaih, have been recorded from the latest Cretaceous and Early Paleocene beds of Saudi Arabia (Al-Furaih, 1980).

From the analyses given above it is apparent that the majority of the ostracodes are either new or have so far been known from the Inter-trappean beds of the east coast of India. One species, *X. subglobosa*, occurs widely in the Eocene beds. Four species, *B. beraguaensis*, *C. bhatiai*, *P. indica*, and *P. khuialaensis*, were originally reported from the lower Eocene beds, and two species, *H. bassiporosa* and *N. diluta*, are characteristic of Early Paleocene age. So far as the Early Eocene species are concerned, it is feared that the stratigraphic horizons from where the occurrences of these species were reported; i.e. Fuller's Earth at Palana, Bikaner District, Rajasthan (Khosla, 1972), Kakdi Stage, Kachchh District (Khosla and Pant, 1988), and sub-surface samples from Vridhachalam District (Guha and Shukla, 1974), have not been precisely dated on the basis of planktonic foraminifers and might be of Paleocene age. The presence of *H. bassiporosa* and *N. diluta* in the Inter-trappean beds of the east coast of India is suggestive of an Early Paleocene age for the beds.

This is in conformity with the views of Bhandari (1995), who has proposed an Early Paleocene age for these beds on the basis of similarity of their ostracode fauna with the ostracodes of the Karimpur Member of the Ghatal Formation of Dhananjapur Well No. 1, West Bengal Basin. In the Karimpur Member ostracodes are associated with a few planktonic foraminifers like *Morozovella pseudobulloides* and smaller benthics like *Protelphidium adamsi*, *Discorbis midwayensis* var. *soldadoensis* etc., suggesting an Early Paleocene (Danian) age (= 1PB on Planktic scale).

### Paleoenvironments

The Inter-trappean beds of the Rajahmundry area (as is true of other coastal formations in India) are the result of a marine transgression, which took place in Early Paleocene times. The paleoenvironment of the beds is discussed on the basis of evidence furnished by ostracodes.

**Table 4.** Distribution of ostracodes in the Inter-trappean beds of the east coast of India.

Horizon	Sample number																		Total	
	Section I											Section II								
	1	2	3	4	5	6	7	8	9	10	11	1	2	3	4	5	6	7		8
<i>Bairdia beraguaensis</i> Singh & Tewari																			1	
<i>Costabuntonia hartmanni</i> (Jain)						3	4	2	42	4	2			3				16	6	82
<i>Cushmanidea bhatiai</i> Bhandari											2	1	1	10				4		18
<i>Cytherella mohani</i> Bhandari														3				11	6	20
<i>Cytherella</i> sp. A																		4		4
<i>Cytherella</i> sp. B																		1		1
<i>Cytherelloidea bhatiai</i> Guha & Shukla									1									5	1	7
<i>Cytheromorpha godavariensis</i> sp. nov.						2					1	14	75	35						127
<i>Cytherura duddukuruensis</i> sp. nov.									3	29	9	8	106	136				18		309
<i>Falsocythere elongata</i> (Bhalla)							4					1						35		40
<i>Paijenborchellini</i> gen. et sp. indet. A					2	1														3
<i>Hapsicytheridea undulata</i> sp. nov.						1			2	34	6	37	164	105	4				11	364
<i>Hermanites sastryi</i> Bhalla					6	10			31	3		4	7					38	3	102
<i>Holcopocythere bassiporosa</i> Al-Furaih						18			2				4							24
<i>Hornibrookella tewarii</i> (Bhalla)									16	24			2				4	69	33	148
<i>Krithe bhandarii</i> sp. nov.									4	2	2	25	76	138				17		264
<i>Munseyella indica</i> sp. nov.									1									6		7
<i>Neocyprideis raoi</i> (Jain)				85	203	304	418	38	53	12	10	211	360	130			41	69		1934
<i>Neomonoceratina paraoertlii</i> sp. nov.							1					39	143	92						275
<i>Nucleolina diluta</i> Al-Furaih																		8	10	18
<i>Paijenborchellina indica</i> (Khosla)																		24		24
<i>Palmoconcha rajui</i> Bhandari						5	3		2	51	8	2	6	4					38	119
<i>Paracandona andhraensis</i> sp. nov.			10																	10
<i>Paracypris khuialaensis</i> Bhandari												8	4					4		16
<i>Semicytherura diluta</i> sp. nov.												33	63	14						110
<i>Uroleberis rasilis</i> sp. nov.																		3		3
<i>Xestoleberis subglobosa</i> (Bosquet)										3								7		10
TOTAL	0	0	10	85	211	344	430	40	157	162	40	383	1017	664	4	0	45	339	109	4040

### Section I

In Section I ostracodes make their first appearance in grey clay (Sample No. 3) where they are represented by a solitary species of *Paracandona*. The underlying beds, in ascending order, light yellow limestone (Sample No. 1) and greyish-white clay (Sample No. 2) are devoid of ostracode fauna. *Paracandona* is a characteristic freshwater genus. Its occurrence in the grey clay suggests that the bed might have accumulated in a similar environment.

In the succeeding brownish-yellow marl (lower part, Sample No. 4) appears a species of *Neocyprideis*, which occurs commonly in it. Soon, however, the species becomes enormously abundant in the overlying beds. In brownish-yellow marl (upper part, Sample No. 5) it constitutes 97% of the entire ostracode assemblage, while in yellowish-grey clay, sample Nos. 6 and 7, it forms 84% and 98% respectively. The other ostracodes present in their order of predominance are *Hermanites*, *Costabuntonia*, *Holcopocythere*, Genus A, *Palmoconcha*, *Cytheromorpha*, *Hapsicytheridea* and *Neomonoceratina*.

Of these ostracodes, little is known about the ecology of

the genera *Costabuntonia*, Genus A, *Holcopocythere* and *Hapsicytheridea* as they do not occur in the present day. The genera *Hermanites* and *Neomonoceratina* are epineritic and the genus *Cytheromorpha* is characteristic of mesohaline to littoral environments (Morkhoven, 1963). A Recent species of *Palmoconcha* has been described by Swain and Gilby (1974) from Station I, Bahia Sebastian Vizcaino, Baja California at a depth of 59 m. The genus *Neocyprideis* is closely related to the living genus *Cyprideis*, which probably evolved from it (Morkhoven, 1963). The latter genus inhabits freshwater to hypersaline conditions, but is most abundant in mesohaline salinities and hence is regarded as the most typical brackish-water ostracode. According to Keij (1957), Morkhoven (1963), Oertli (1967), Keen (1977) and Neale (1988), *Neocyprideis* also occurs predominantly in brackish-water environments. Keen (1977) records the genus from three brackish-water assemblages, maximum predominance being in assemblage IV of the Upper Eocene beds of the Hampshire Basin, U. K. Assemblage IV is taken to represent salinities of 9.0 to 16.5‰. Neale (1988) has observed that minimum di-



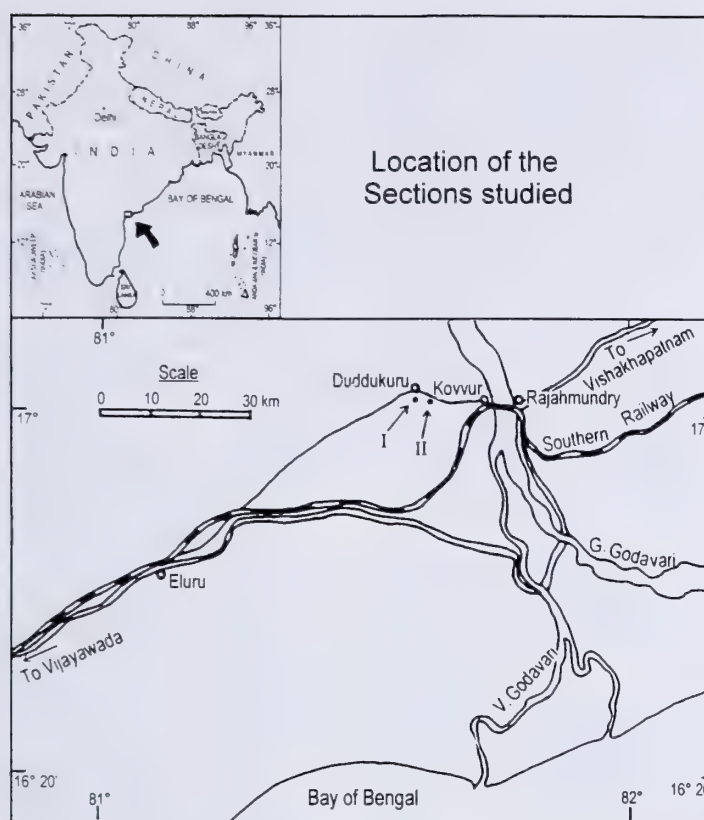


Figure 1. Index map of part of Andhra Pradesh showing locations of the sections studied.

versity of species and abundance of individuals and reached in low brackish-water environments. In the present Sample Nos. 4–7 of Section I *Neocyprideis* constitute a very high proportion of the ostracode assemblages (84 to 100%) and other ostracodes together form small fractions, suggesting that the brownish yellow marl and yellowish-grey clay were deposited in a mesohaline (9 to 16.5‰), outer bay environment.

There is a sharp decline both in diversity as well as frequency of ostracode fauna in the overlying light yellow limestone (Sample No. 8). Only two species of *Neocyprideis* and *Costabuntonia* are encountered in this bed suggesting a temporary shallowing of the basin, and the bed might have been deposited in the marginal estuarine environments. This view is further corroborated by disappearance of foraminifers except for some *Nonion*. Megafossils are represented by *Ostrea*, characteristic of near-shore environments.

There was again an influx of a large number of ostracode species in the succeeding yellowish-grey clay (Sample No. 9) and light yellow limestone (Sample Nos. 10 and 11). The ostracodes in order of predominance are: *Neocyprideis*, *Palmoconcha*, *Cytherura*, *Costabuntonia*, *Hermani-*

*tes*, *Hapsicytheridea*, *Hornibrookella*, *Krithe*, *Cushmani-*  
*dea*, *Cytherelloidea*, *Cytheromorpha*, *Falsocythere*, *Hol-*  
*pocythere*, *Munseyella* and *Xestoleberis*. Of these, eight genera appear for the first time. Their ecological significance is as follows. The genus *Hornibrookella* is extinct and therefore little is known about its ecology. The genus *Cytherelloidea* inhabits shallow, warm marine waters; occasionally it is also found in brackish-water (mesohaline) environments (Morkhoven, 1963). According to Sohn (1964), the genus is a good paleotemperature indicator and in the present-day seas it does not survive in temperatures less than 10 °C. The genus *Cytherura* inhabits mesohaline to littoral environments (Morkhoven, 1963). The genus *Falsocythere* is a shallow marine form. A living species of the genus has been described from the coastal waters of the Adriatic Seas by Bonaduce *et al.* (1975) and the Gulf of Aquaba (Red Sea) by Bonaduce *et al.* (1980). There is some difference of opinion about the ecology of the genus *Krithe*. According to van den Bold (1960), it occurs in a near-shore as well as an open-shore facies, while Morkhoven (1963) is of the view that the genus is strictly marine and most commonly occurs in infraneritic to bathyal environments. The genus *Munseyella* thrives well in an

epineritic environment predominantly in warmer waters (Morkhoven, 1963). Studies of living species of *Cushmanidea* by Ascoli (1964) and McKenzie and Swain (1967) suggest that the genus inhabits lagoonal to shallow-water environments. Keen (1977) records it from the assemblage V (polyhaline, 16.5 to 33‰) of the Upper Eocene beds of Hampshire, U.K.

Ecological significance of the genera *Neocyprideis*, *Palmoconcha*, *Hermanites* and *Cytheromorpha* has already been discussed. In the present beds under discussion the frequency of *Neocyprideis* declines considerably as compared to underlying beds (Sample Nos. 4 to 7) and the appearance of a number of marine genera suggests that the yellowish-grey clay and light yellow limestone might have been deposited in a polyhaline bay (16.5 to 33 ‰).

## Section II

The section II is only 2.41 meters thick and comprises, in ascending order, light yellow limestone (Sample Nos. 1 to 4), grey clay (Sample No. 5) and greyish-white limestone (Sample Nos. 6–8). The ostracode fauna in the section is much varied and of high frequency in the lower and upper limestone beds, but absent in the middle grey clay. This succession corresponds with the upper part of the succession in Section I (i.e. yellowish-grey clay and light yellow limestone). The paleoecology of the ostracodes in Section II is discussed below.

The ostracodes in the light yellow limestone (Sample Nos. 1–4) in their order of predominance are *Neocyprideis*, *Hapsicytheridea*, *Neomonoceratina*, *Cytherura*, *Krihe*, *Cytheromorpha*, *Semicytherura*, *Costabuntonia*, *Cushmanidea*, *Palmoconcha*, *Hermanites*, *Paracypris*, *Cytherella*, *Falsocythere*, *Holcopocythere* and *Hornibrookella*.

The genera *Cytherella*, *Paracypris* and *Semicytherura* appear for the first time in this bed. These are essentially marine genera (Morkhoven, 1963). The genus *Cytherella* occurs at all depths and rarely is also found in brackish-water (mesohaline) environments. The genus *Paracypris* mainly occurs in deeper water but is very rare in occurrence, and hence may not be of much significance. The genus *Semicytherura* is epineritic, predominantly littoral. The high diversity of shallow marine genera and presence of *Neocyprideis* in large numbers suggest that the limestone bed might have accumulated in a polyhaline-bay, brackish-water environment similar to the top two beds of Section I.

The overlying grey clay (Sample No. 5) is devoid of ostracodes. Possibly there was a temporary shallowing of the basin and the bed was deposited in marginal estuarine environments similar to the light yellow limestone (Sample no. 8) of Section I.

The succeeding greyish white limestone is again rich in ostracode fauna. It is represented in order of dominance

by *Hornibrookella*, *Neocyprideis*, *Costabuntonia*, *Hermanites*, *Falsocythere*, *Palmoconcha*, *Cytherella*, *Cytherura*, *Hapsicytheridea*, *Krihe*, *Xestoleberis*, *Paijenborchellina*, *Cytherelloidea*, *Nucleolina*, *Bairdia*, *Cushmanidea*, *Munseyella*, *Paracypris* and *Uroleberis*.

The genera *Paijenborchellina*, *Nucleolina*, *Bairdia* and *Uroleberis* appear for the first time in this bed. The genus *Nucleolina* does not extend in the present day. Therefore little is known about its ecological significance. Studies of certain living species of the genus *Paijenborchellina* from the Abu Dhabi lagoon, Persian Gulf (Bate, 1971) show that it occurs from littoral to near-shore shelf environments. The genus *Bairdia* is a characteristic marine form occurring both in very shallow as well as very deep waters (Morkhoven, 1963). In the present day the genus *Uroleberis* occurs in epineritic environments (Morkhoven, 1963). The ecological significance of other genera has already been discussed.

Like the light yellow limestone (Sample Nos. 1–4) of Section II and the upper two beds of Section I, the present bed is characterised by varied shallow marine ostracodes, suggesting that it was also deposited in a polyhaline bay.

The paleoenvironmental inferences drawn above are more or less similar to those of Bhalla (1967) and Bhandari (1995) who also worked on the Inter-trappean beds of this region. According to Bhalla (1967), the foraminiferal and ostracode assemblages reflect rhythmic facies changes with alternate brackish-water and normal marine environments of deposition. He also recorded two marine incursions in the area. Bhandari (1995) inferred that the Inter-trappean beds of Duddukuru were deposited in brackish-water to shallow inner neritic conditions around 0–10 m deep with intermittent freshwater conditions.

## Systematic paleontology

The classification of ostracodes in this paper follows that of Hartmann and Puri (1974). Descriptions of already known and well established species are omitted for the sake of brevity. The illustrated specimens are deposited in the museum of the Department of Geology, Mohan Lal Sukhadia University, Udaipur and catalogued with the prefix SUGDMF.

Order Podocopida  
Suborder Platycopa  
Family Cytherellidae  
Genus *Cytherella* Jones, 1849

*Type species.*—*Cytherina ovata* Roemer, 1840.



*Cytherella* sp. A

Figure 2.3

*Cytherella* sp. cf. *muensteri* (Roemer). Jain, 1978, p. 52, pl. 1, fig. 1.

**Material.**—Four carapaces.

**Remarks.**—The species was recorded as *Cytherella* sp. cf. *muensteri* by Jain (1978) from the Inter-trappean beds of Kateru, Rajahmundry. It, however, differs from *Cytherella muensteri* (Roemer) in having an angulated dorsal margin, the greatest height located near the middle, and a smooth surface. *C. muensteri*, in contrast, has the greatest height located at the posterior 1/3 of the length, has a pitted surface, and lacks the dorsal angulation. The species is left under open nomenclature.

**Dimensions.**—A carapace, SUGDMF no. 565, length 0.69 mm, height 0.42 mm, width 0.27 mm.

**Occurrence.**—Section II.

*Cytherella* sp. B

Figure 2.4

**Material.**—One carapace.

**Description.**—Carapace subrectangular in lateral outline; height equal in anterior and posterior halves; right valve slightly overlaps left valve along dorsal and ventral margins; dorsal margin nearly straight; ventral margin slightly concave, anterior and posterior margins rounded; valve surface smooth.

**Remarks.**—This species differs from *Cytherella mohani* Bhandari, 1995 and *Cytherella* sp. A recorded herein in the lateral outline and degree of overlap. *C. mohani* is subovate in shape with a pronounced overlap, while *Cytherella* sp. A is an elongate form having an angulated dorsal margin. The present species is left under open nomenclature.

**Dimensions.**—A carapace, SUGDMF no. 566, length 0.74 mm, height 0.42 mm, width 0.32.

**Occurrence.**—Section II.

Genus *Cytherelloidea* Alexander, 1929

**Type species.**—*Cythere* (*Cytherella*) *williamsoniana* Jones, 1849.

*Cytherelloidea bhatiai* Guha and Shukla, 1974

Figure 2.5

*Cytherelloidea bhatiae* Guha and Shukla, 1974, p. 96, 97, pl. 2, fig. 10.

*Cytherelloidea* sp. cf. *C. keiji* McKenzie. Jain, 1978, p. 52, 53, pl. 1, figs. 2, 3. Bhandari, 1995, p. 94, pl. 1, fig. 3.

**Material.**—Seven carapaces.

**Description.**—Carapace subrectangular in lateral outline, with height equal in both anterior and posterior halves; valve surface ornamented by elongate punctation; two prominent, sinuate, transverse ridges extending three-fourths of length joined by a posterior vertical ridge; and marginal rim along dorsal, anterior and ventral margins.

**Remarks.**—The present specimens from Duddukuru are referred to *Cytherelloidea bhatiai* Guha and Shukla (1974) (species name misspelled as *bhatiae*) described from the Lower Eocene of Gopurapuram well, Vridhachalam, Tamilnadu. The form described as *Cytherelloidea* sp. cf. *C. keiji* from the Inter-trappean beds of the east coast of India by Jain (1978) and Bhandari (1995) belongs to this species. According to McKenzie *et al.* (1990) *Keijcyoidea keiji* (earlier referred to *Cytherelloidea*) is a Pleistocene-Recent species ranging in distribution from the southwestern Pacific to northwestern and southern Australia.

**Dimensions.**—A carapace, SUGDMF no. 567, length 0.48 mm, height 0.29 mm, width 0.21 mm.

**Occurrence.**—Sections I and II.

Suborder Podocopa  
Superfamily Cytheracea  
Family Cytheridae  
Subfamily Cytherinae  
Tribe Cytherini  
Genus *Cytheromorpha* Hirschmann, 1909

**Type species.**—*Cythere fuscata* Brady, 1869.

*Cytheromorpha godavariensis* sp. nov.

Figure 2.7–2.9

**Etymology.**—After the Indian River Godavari.

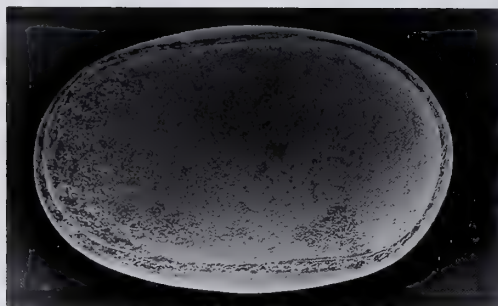
**Material.**—124 carapaces and 3 valves.

**Type locality.**—Light yellow limestone (Sample SUGDMF no. 3/II), Inter-trappean beds, Paleocene, Section II.

**Diagnosis.**—Surface strongly reticulate and with a transverse median ridge.

**Description.**—Carapace subquadrate in lateral outline, with greatest height at anterior cardinal angle; overlap indistinct; valve inflated ventrally; dorsal margin straight converging posteriorly; ventral margin obscured medially; anterior margin broadly rounded; posterior margin much narrower, subangulate near mid-height; in dorsal view carapace somewhat biconvex, both ends taper, more in posterior than in anterior, maximum width posterior to middle. Valve surface strongly reticulate, edges of reticulation meshes in anterior half raised in low costae; a transverse ridge in median region. Inner lamella moderately wide along anterior and posterior margins and narrows ventrally;





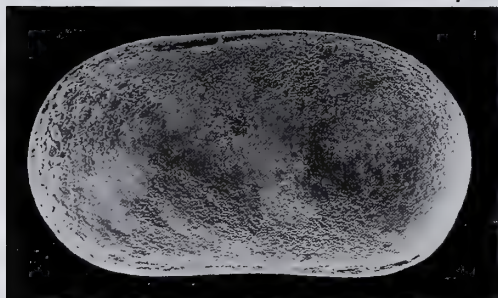
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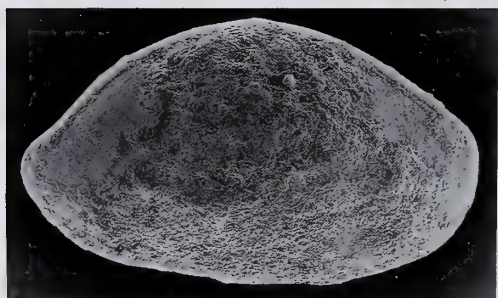
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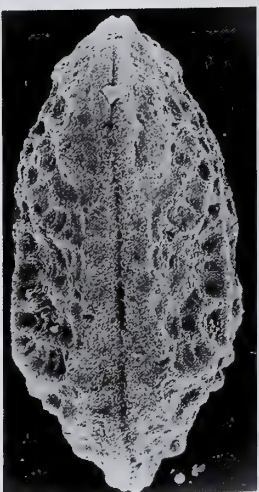
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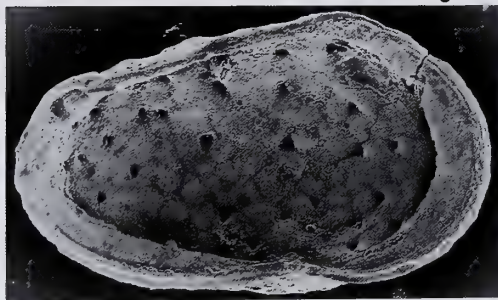
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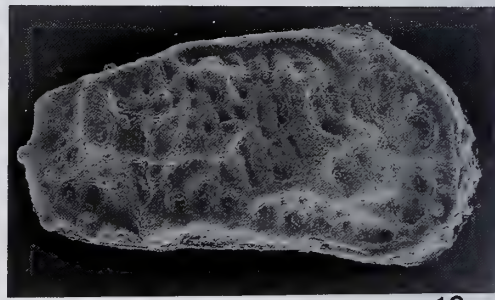
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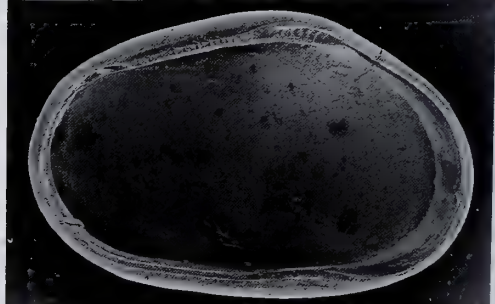
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vestibule present; selvage near outer periphery; normal pores few, widely spaced. Hinge gongyodont; in left valve it consists of an indistinct socket surrounded by a crenulate anterior tooth, which is a continuation of the median crenulate bar and a posterior socket with a distinct tooth at its inner edge.

*Dimensions.*—Holotype, SUGDMF no. 569, a carapace, length 0.30 mm, height 0.19 mm, width 0.14 mm; paratype I, SUGDMF no. 570, a left valve, length 0.32 mm, height 0.19 mm; paratype II, SUGDMF no. 571, a carapace, length 0.30 mm, height 0.18 mm, width 0.16 mm.

*Discussion.*—*Cytheromorpha godavariensis* sp. nov. resembles *Cytheromorpha kirtharensis* Guha (1968) described from the Middle Eocene of Kachchh in general appearance. *C. kirtharensis*, however, differs from the present species in having concentrically arranged reticulation and a lack of median transverse ridge. *Cytheromorpha bulla* Haskin (1971) described from the Tertiary beds of the Isle of Wight also resembles *C. godavariensis* sp. nov. in overall lateral outline and surface ornamentation but differs in having three distinct vertical ridges in the anterior half.

*Occurrence.*—Sections I and II.

#### Tribe Pectocytherini

Genus *Munseyella* van den Bold, 1957

Type species.—*Toulminia hyalokystis* Munsey, 1953.

#### *Munseyella indica* sp. nov.

Figure 2.10, 2.11

*Etymology.*—After the country of India.

*Material.*—Six carapaces and one valve.

*Type locality.*—Greyish-white limestone (Sample SUGDMF no. 7/II), Inter-trappean beds, Paleocene, Section II.

*Diagnosis.*—Surface ornamented by ridges and vertically arranged pits.

*Description.*—Carapace subquadrate in lateral outline, with greatest height about half of length at anterior cardinal angle; posterior cardinal angle well marked; valves almost equal; dorsal margin nearly straight, sloping down posteriorly; ventral margin concave; anterior margin broadly rounded; posterior straight, nearly perpendicular to

ventral margin; anterior margin fringed with 6 or 7 spines and posterior margin with two spines, one at mid-posterior and the other at posteroventral region; in dorsal view carapace rather compressed. Valve surface ornamented by anterior marginal ridge which also continues ventrally slightly above margin; a dorsal ridge extending from anterior cardinal angle backward overhanging margin, in posterodorsal region it turns downward forming a thick knob; two short furcating transverse ridges, one in posteromedian-median region and the other in ventromedian-anterioventral region; a vertical ridge extending downward from anterodorsal region; vertically arranged deep elongate pits over rest of area.

*Dimensions.*—Holotype, SUGDMF no. 572, a right valve, length 0.38 mm, height 0.21 mm; paratype, SUGDMF no. 573, a carapace, length 0.42 mm, height 0.22 mm, width 0.19 mm.

*Discussion.*—The species closely resembles *Munseyella japonica* (Hanai, 1957), a Recent species from Kanagawa Prefecture, Japan in overall shape but differs in surface ridge pattern and having vertically arranged, elongate pits.

*Occurrence.*—Sections I and II.

#### Tribe Paijenborchellini

Genus *Neomonoceratina* Kingma, 1948

Type species.—*Neomonoceratina columbiformis* Kingma, 1948.

#### *Neomonoceratina paraoertlii* sp. nov.

Figure 3.1, 3.2

*Etymology.*—From Greek *para*, meaning “beside,” with reference to its resemblance with *Neomonoceratina oertlii* Guha, 1967.

*Material.*—275 carapaces.

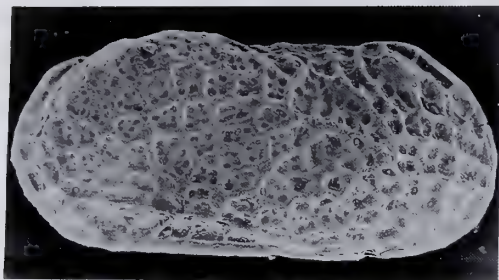
*Type locality.*—Light yellow limestone (Sample SUGDMF no. 3/II), Inter-trappean beds, Paleocene, Section II.

*Diagnosis.*—Surface distinctly reticulate, meshes with 5 or 6 pores, and a depression between ventral ridge and margin.

*Description.*—Carapace elongate, subrectangular in lateral outline, height almost equal in anterior and posterior halves; overlap indistinct; dorsal margin nearly straight

◀ **Figure 2.** 1, 2. *Cytherella mohani* Bhandari. 1, carapace, SUGDMF no. 563, left valve view,  $\times 78$ ; 2, carapace, SUGDMF no. 564, dorsal view,  $\times 80$ . 3. *Cytherella* sp. A, carapace, SUGDMF no. 565, left valve view,  $\times 83$ . 4. *Cytherella* sp. B, carapace, SUGDMF no. 566, left valve view,  $\times 81$ . 5. *Cytherelloidea bhatiai* Guha and Shukla, carapace, SUGDMF no. 567, left valve view,  $\times 123$ . 6. *Bairdia beraguaensis* Singh and Tewari, carapace, SUGDMF no. 568, right valve view,  $\times 76$ . 7–9. *Cytheromorpha godavariensis* sp. nov. 7, holotype, SUGDMF no. 569, carapace, right valve view,  $\times 210$ ; 8, paratype I, SUGDMF no. 570, left valve, internal view,  $\times 200$ ; 9, paratype II, SUGDMF no. 571, carapace, dorsal view,  $\times 213$ . 10, 11. *Munseyella indica* sp. nov. 10, holotype, SUGDMF no. 572, right valve, lateral view,  $\times 166$ ; 11, paratype, SUGDMF no. 573, carapace, dorsal view,  $\times 152$ . 12, 13. *Neocyprideis raoi* (Jain). 12, carapace, SUGDMF no. 579, right valve view,  $\times 80$ ; 13, left valve, SUGDMF no. 580, internal view,  $\times 81$ .

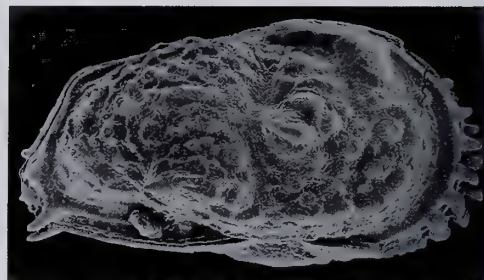




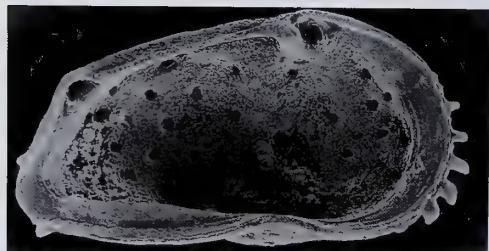
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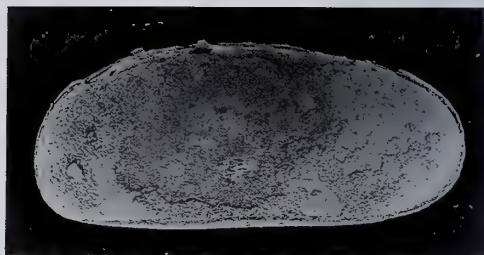
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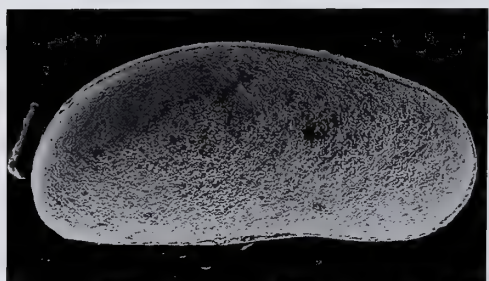
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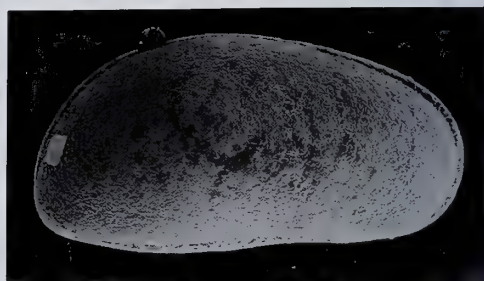
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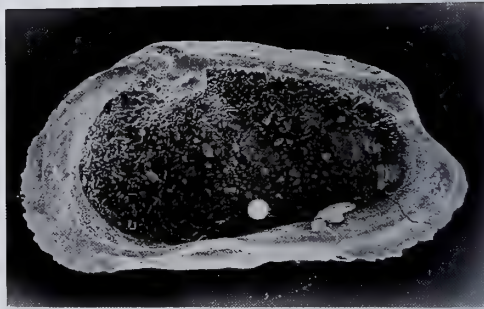
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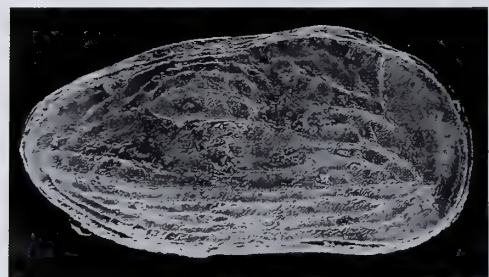
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anteriorly and with a distinct hump posteriorly, obscuring margin; ventral margin straight; anterior margin broadly rounded; posterior margin less so; in dorsal view ends compressed, sides more or less parallel. Eye tubercle present. Valve surface marked by a shallow depression in mid-dorsal and dorsomedian regions; distinct reticulation, meshes mostly quadrangular in shape and with 5 or 6 pores; three feeble longitudinal ridges, median ridge extending from mid-anterior region to posteromedian region, ventral ridges nearly parallel, sloping up and back from mid-ventral region; and a prominent depression between ventral ridge and margin. Internal characters not known.

*Dimensions*.—Holotype, SUGDMF no. 574, a carapace, length 0.42 mm, height 0.19 mm, width 0.18 mm; paratype, SUGDMF no. 575, a carapace, length 0.40 mm, height 0.19 mm, width 0.19 mm.

*Discussion*.—The species very closely resembles *Neomonoceratina oertlii* Guha (1967) from the Miocene of Saurashtra, Gujarat in lateral outline and overall surface ornamentation. The latter species, however, differs in being much larger in size and having a distinct vertical sulcus.

*Occurrence*.—Sections I and II.

Paijenborchellini gen. et sp. indet. A

Figure 3.3–3.5

*Material*.—One carapace and two valves.

*Description*.—Carapace elongate, subtrapezoidal in lateral outline, with greatest height about half of length at anterior cardinal angle; left valve slightly overlaps right valve along anterodorsal and posteroventral margins; valves somewhat inflated ventrally, overhanging margin in median and anteroventral region; dorsal margin straight, converging backward; posterior cardinal angle well marked; anterior margin broad, obliquely rounded and fringed with 5 large, downwardly curved spines; posterior margin drawn out ventrally and fringed with two spines; in dorsal view carapace sagittate, distinctly compressed near anterior and posterior ends. Valve surface strongly tuberculate, superimposed by punctation, and marked by a row of about 10 tubercles extending from mid-anterior to mid-ventral region, with a subcentral swelling and a vertical sulcus posterior to it. Inner lamella moderately wide; line of concrescence and inner margin coincide; selvage periph-

eral; normal pore widely scattered; central muscle scars comprise a vertical row of four scars, lowest being largest, frontal scar not known. Hinge schizodont; in left valve it consists of an anterior socket with two loculi, a postadjacent bilobate anteromedian tooth, a long crenulate posteromedian bar and a large posterior socket, open interiorly; hinge complementary in right valve, anterior tooth bilobate, posterior tooth indistinctly crenulate.

*Remarks*.—The species probably belongs to a new genus but no name is proposed because of insufficient material.

*Dimensions*.—A carapace, SUGDMF no. 576, length 0.62 mm, height 0.32 mm, width 0.27 mm; a left valve, SUGDMF no. 577, length 0.62 mm, height 0.32 mm; a right valve, SUGDMF no. 578, length 0.61 mm, height 0.32 mm.

*Occurrence*.—Section I.

Family Cytherideidae  
Subfamily Cytherideinae  
Genus *Neocyprideis* Apostolescu, 1957

*Type species*.—*Cyprideis* (*Neocyprideis*) *durocortorien-sis* Apostolescu, 1957.

*Neocyprideis raoi* (Jain, 1978)

Figure 2.12, 2.13

*Ovocytheridea raoi* Jain, 1978, p. 53, pl. 1, figs. 7–10; Bhandari, 1995, p. 95, 96, pl. 2, figs. 1, 2.

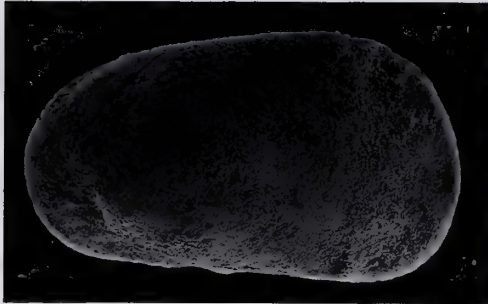
*Material*.—1134 carapaces and 800 valves.

*Remarks*.—The species has previously been described as *Ovocytheridea raoi* Jain (1978) from the Inter-trappean beds of Kateru, Rajahmundry and from Duddukuru, West Godavari District, Andhra Pradesh (Bhandari, 1995). This is the most abundant species in our collection and in certain samples it constitutes up to 90 percent of the total ostracode population.

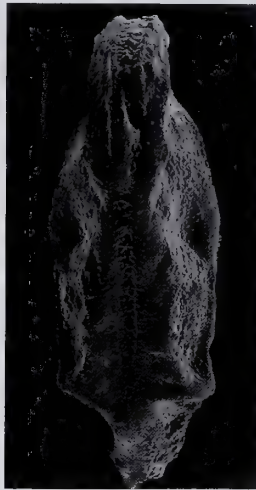
*Ovocytheridea* is essentially a Cretaceous genus and the majority of the described species of the genus have a trianguloid lateral outline, strongly convex dorsal margin, posterior margin steeply down-sloping and narrowly ventrally rounded, generally smooth valve surface, narrow median hinge element, distinct accommodation groove, and frontal scars that comprise two closely spaced scars. In

◀ **Figure 3.** 1, 2. *Neomonoceratina paraoertlii* sp. nov. 1, holotype, SUGDMF no. 574, carapace, right valve view,  $\times 157$ ; 2, paratype, SUGDMF no. 575, carapace, dorsal view,  $\times 152$ . 3–5. *Paijenborchellini* gen. et sp. indet. A. 3, carapace, SUGDMF no. 576, right valve view,  $\times 102$ ; 4, left valve, SUGDMF no. 577, internal view,  $\times 100$ ; 5, right valve, SUGDMF no. 578, dorsal view,  $\times 105$ . 6. *Cushmanidea bhatiai* Bhandari, carapace, SUGDMF no. 581, right valve view,  $\times 72$ . 7, 8. *Krithe bhandarii* sp. nov. 7, holotype, SUGDMF no. 582, male carapace, right valve view,  $\times 142$ ; 8, paratype, SUGDMF no. 583, female carapace, right valve view,  $\times 147$ . 9–11. *Holcopocythere bassiporosa* Al-Furaih. 9, left valve, SUGDMF no. 584, lateral view,  $\times 111$ ; 10, right valve, SUGDMF no. 585, internal view,  $\times 113$ ; 11, carapace, SUGDMF no. 586, dorsal view,  $\times 120$ . 12, 13. *Cos-tabuntonia hartmanni* (Jain). 12, female carapace, SUGDMF no. 554, right valve view,  $\times 90$ ; 13, male carapace, SUGDMF no. 557, right valve view,  $\times 87$ .

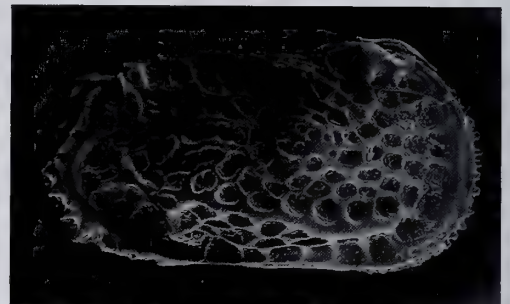




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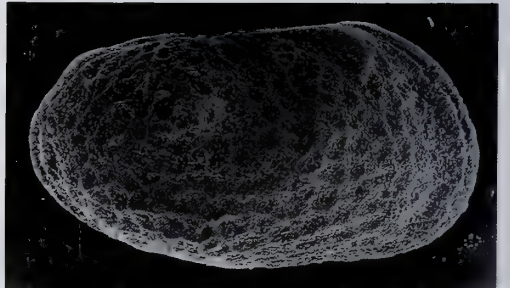
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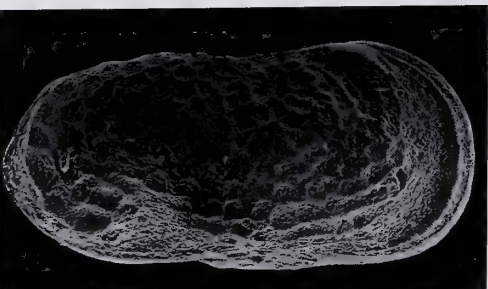
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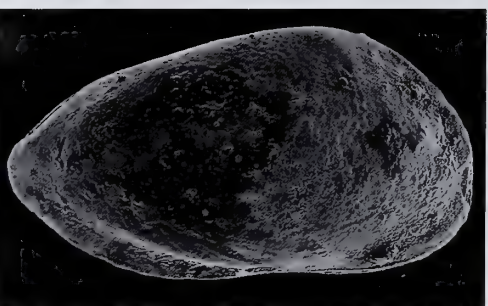
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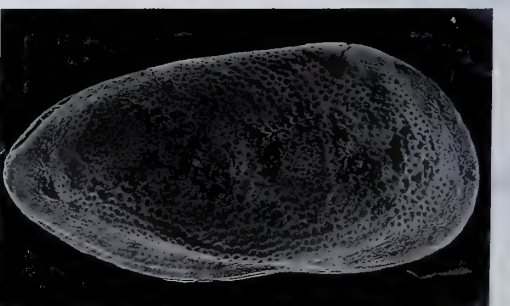
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contrast to this pattern the present species has an elongate and subovate lateral outline, the greatest height slightly anterior to the middle, dorsal margin arched, anterior and posterior margins evenly rounded, median hinge element quite wide, accommodation groove almost lacking, and frontal scar typically v-shaped.

The species is very similar to *Neocyprideis bhupendri* Singh and Mishra (1968) from the Lower Eocene of Rajasthan in all the essential carapace characters (see also Khosla, 1972). This species is also recorded from the Middle Eocene of Kachchh by Khosla and Pant (1988) and the Middle Eocene of Meghalaya by Bhandari (1992). Restudy of the type material of *N. bhupendri* is required to clarify the identity with the present species. The species also closely resembles *Neocyprideis simplex* Siddiqui (2000) from the Lower Eocene of Pakistan in lateral outline and ornamentation. On the basis of the characters given above the present species is transferred to the genus *Neocyprideis*.

**Dimensions.**—A carapace, SUGDMF no. 579, length 0.75 mm, height 0.48 mm, width 0.40 mm; a left valve, SUGDMF no. 580, length 0.75 mm, height 0.50 mm.

**Occurrence.**—Sections I and II.

#### Family Krithidae

Genus *Krithe* Brady, Crosskey and Robertson, 1874

**Type species.**—*Ilyobates praetexta* Sars, 1866.

#### *Krithe bhandarii* sp. nov.

Figure 3.7, 3.8

**Etymology.**—The species is named in honor of Dr. Anil Bhandari, Chief Geologist, Micropaleontology Laboratory, KDMIPE, ONGC Ltd., Deharadun, India.

**Material.**—264 carapaces.

**Type locality.**—Light yellow limestone (Sample SUGDMF no. 3/II), Inter-trappean beds, Paleocene. Section II.

**Diagnosis.**—Carapace elongate, with greatest height posterior to middle; ventral margin concave anteriorly; posterior margin forming obtuse angle with ventral margin.

**Description.**—Sexual dimorphism distinct, males being more elongate, less high and wide than females. Carapace

elongate, subrectangular in lateral outline, with greatest height almost half of length posterior to middle; left valve overlaps right valve along dorsal, anterior and mid-ventral margins; dorsal margin asymmetrically convex, merges gradually with anterior margin, and steeply sloping downward from posterior 2/5 of length; ventral margin with a distinct concavity anterior to middle; anterior margin narrow, evenly rounded; posterior obliquely rounded forming obtuse angle with ventral margin; in dorsal view carapace compressed with maximum width near middle. Valve surface smooth.

**Dimensions.**—Holotype, SUGDMF no. 582, a male carapace, length 0.43 mm, height 0.22 mm, width 0.19 mm; paratype, SUGDMF no. 583, a female carapace, length 0.40 mm, height 0.24 mm, width 0.19 mm.

**Discussion.**—*Krithe bhandarii* sp. nov. resembles *Krithe oryza* Neale and Singh (1985) and *Krithe* cf. *K. oryza* from the Middle Eocene of Assam in having a vaulted dorsal margin but is readily differentiated in having a distinct concavity along the ventral margin and different outline of the posterior margin.

**Occurrence.**—Sections I and II.

#### Family Hemicytheridae

##### Subfamily Orionininae

Genus *Falsocythere* Ruggieri, 1972

**Type species.**—*Falsocythere maccagno* (Ciampo, 1972) Ruggieri, 1972.

#### *Falsocythere elongata* (Bhalla, 1979)

Figure 4.5, 4.6

*Occultocythereis elongatum* Bhalla, 1979c, p. 146–148, figs. A–D.

**Material.**—40 carapaces.

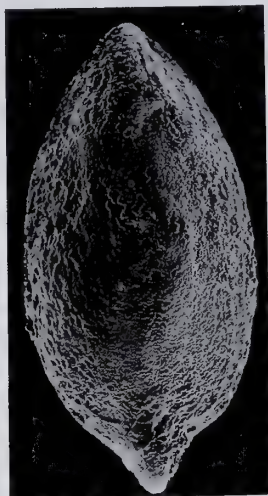
**Description.**—Carapace elongate subquadrate in lateral outline, with greatest height about half of length at anterior cardinal angle and greatest length at ventral one-third of height; dorsal margin partly obscured due to overhanging ridge, otherwise straight, sloping down posteriorly; ventral margin slightly concave; anterior margin broadly rounded; posterior margin much narrowed, drawn out ventrally, distinctly concave in upper part and obliquely truncated in lower part; anterior and posterior margins denticulate;

← **Figure 4.** 1. *Nucleolina diluta* Al-Furaih, carapace, SUGDMF no. 587, right valve view,  $\times 84$ . 2, 3. *Hermanites sastryi* Bhalla. 2, carapace, SUGDMF no. 588, right valve view,  $\times 64$ ; 3, right valve, juvenile, SUGDMF no. 589, lateral view,  $\times 80$ . 4. *Hornibrookella tewarii* (Bhalla), carapace, SUGDMF no. 590, right valve view,  $\times 86$ . 5–6. *Falsocythere elongata* (Bhalla). 5, carapace, SUGDMF no. 591, right valve view,  $\times 110$ ; 6, carapace, SUGDMF no. 592, dorsal view,  $\times 119$ . 7. *Palmoconcha rajui* Bhandari, carapace, SUGDMF no. 593, right valve view,  $\times 122$ . 8–10. *Hapsicytheridea undulata* sp. nov. 8, holotype, SUGDMF no. 594, carapace, right valve view,  $\times 121$ ; 9, paratype I, SUGDMF no. 595, carapace, dorsal view,  $\times 123$ ; 10, paratype II, SUGDMF no. 596, right valve, internal view,  $\times 122$ . 11–13. *Cytherura duddukuruensis* sp. nov. 11, holotype, SUGDMF no. 597, female carapace, right valve view,  $\times 157$ ; 12, paratype I, SUGDMF no. 598, female carapace, dorsal view,  $\times 155$ ; 13, paratype II, SUGDMF no. 599, male carapace, right valve view,  $\times 155$ .

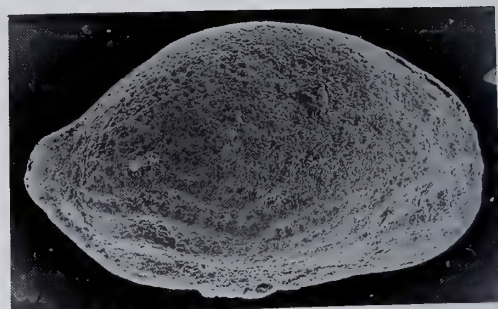




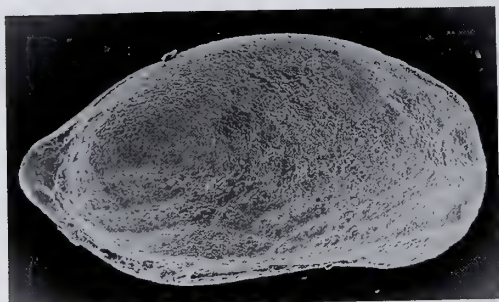
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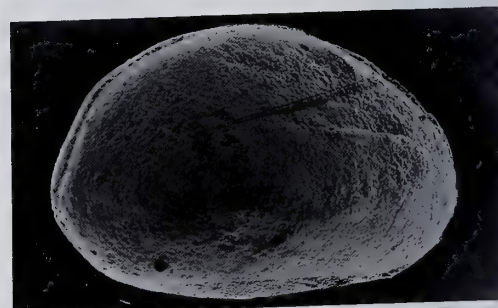
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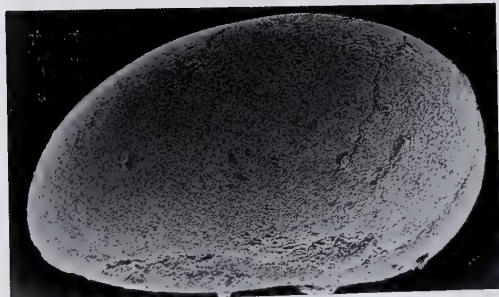
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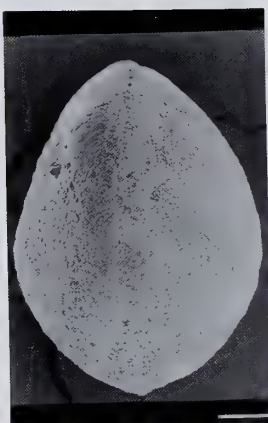
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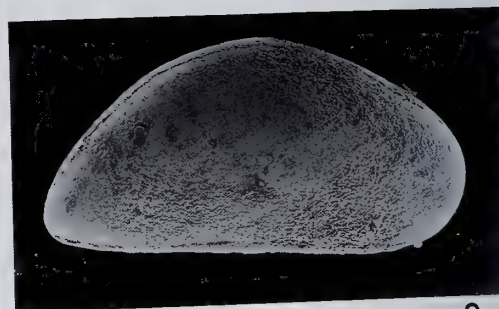
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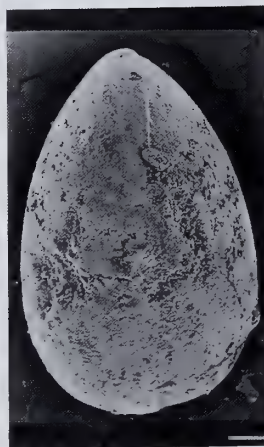
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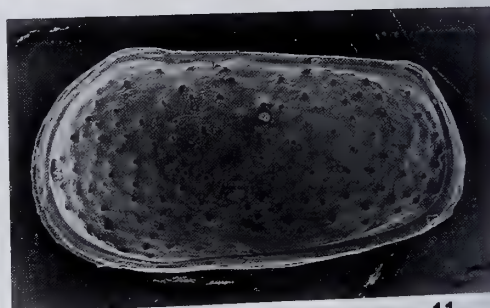
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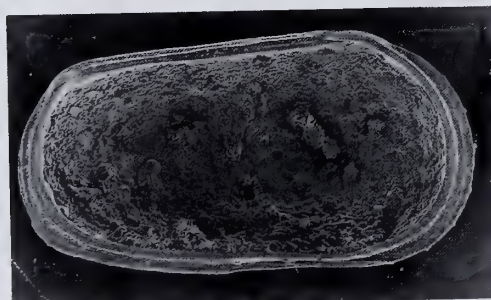
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12



13



valve surface ornamented by a high anterior marginal rim which also continues along ventral and posterior margins; an arched dorsal ridge starting from mid-dorsal region overhangs posterodorsal margin and sharply turns forming a U-shaped bend and then continues as a diagonal ridge to anteromedian region; a low vertical ridge extends downwards from the U-shaped bend; area along marginal rim laterally compressed and smooth; faint reticulation over rest of surface

**Remarks:**—*Occultocythereis elongatum* was described by Bhalla (1979c) from the Inter-trappean beds of Duddukuru. The specimens he illustrated are internal moulds, so that they lack surface reticulation and marginal denticles. The well preserved specimens we newly collected from the type locality allow us to reconsider the generic position of this species.

The lateral outline and surface ornamentation of the species differ from those of the genus *Occultocythereis*. Species of the latter genus generally have a subquadrate lateral outline and a subangular or rounded posterior margin. In addition, they have a valve surface ornamented by 1) a prominent angular massive tubercle at the posterodorsal cardinal angle and a ridge extending from it along the dorsal margin, 2) a prominent anterior rim, 3) a small posteroventral winglike projection with a short vertical ridge posteriorly, and 4) denticles at anterior and posterior margins. Except for having a ventrally drawn-out posterior margin, the present species closely resembles *Falsocythere indica* Khosla and Nagori, 1989, a Lower Miocene species of Kerala, and *F. maccagnoii* (Ciampo, 1972), a Recent species, in overall lateral outline and surface ornamentation. On this basis the species is herein transferred to the genus *Falsocythere*. The difference in the shape of the posterior margin of the present species might be due to the range of variation within the genus.

**Dimensions.**—A carapace, SUGDMF no. 591, length 0.56 mm, height 0.27 mm, width 0.19 mm; a carapace, SUGDMF no. 592, length 0.53 mm, height 0.27 mm, width 0.19 mm.

**Occurrence.**—Sections I and II.

#### Family Loxoconchidae

##### Genus *Palmoconcha* Swain and Gilby, 1974

**Type species.**—*Palmoconcha laevimarginata* Swain and

Gilby, 1974.

##### *Palmoconcha rajui* Bhandari, 1995

Figure 4.7

*Loxoconcha* sp. Jain, 1978, p. 56, pl. 2, figs. 6, 7.

*Palmoconcha rajui* Bhandari, 1995, p. 96, 97, pl. 4, figs. 1–4.

**Material.**—84 carapaces and 35 valves.

**Remarks.**—The present species was described from the Paleocene Inter-trappean beds of Duddukuru by Bhandari (1995). It is based on closed carapaces and its generic assignment is highly questionable. The genus *Palmoconcha* is characterised by the presence of flattened, flangelike terminal marginal areas, a gongylodont hinge, a broad vestibule, and numerous closely spaced short marginal pore canals. In contrast, the present species has an anti-merodont hinge structure; in the left valve the hinge comprises loculate terminal sockets that are connected by a finely crenulate median bar, and in the right valve it is complementary, has a few widely spaced, straight, marginal pore canals and lacks flangelike terminal areas and vestibule. Probably a new generic name is required to accommodate this species, but it is deferred unless additional species are found.

**Dimensions.**—A carapace, SUGDMF no. 593, length 0.51 mm, height 0.29 mm, width 0.29 mm.

**Occurrence.**—Sections I and II.

#### Family Cytheruridae

##### Genus *Hapsicytheridea* Al-Furaih, 1980

**Type species.**—*Hapsicytheridea binodosa* Al-Furaih, 1980.

##### *Hapsicytheridea undulata* sp. nov.

Figure 4.8–4.10

*Cytheridella* sp. Bhandari, 1995, p. 95, pl. 1, fig. 4.

**Etymology.**—From Latin, meaning wavy, referring to sinuous venter surface.

**Material.**—346 carapaces and 18 valves.

**Type locality.**—Light yellow limestone (Sample SUGDMF no. 8/I), Inter-trappean beds, Paleocene.

◀ **Figure 5.** 1. *Paijenborchellina indica* (Khosla), carapace, SUGDMF no. 600, right valve view,  $\times 105$ . 2–4. *Semicytherura diluta* sp. nov. 2, holotype, SUGDMF no. 601, female carapace, right valve view,  $\times 150$ ; 3, paratype I, SUGDMF no. 602, male carapace, right valve view,  $\times 137$ ; 4, paratype II, SUGDMF no. 603, female carapace, dorsal view,  $\times 146$ . 5, 6. *Uroleberis rasilis* sp. nov. 5, holotype, SUGDMF no. 604, carapace, right valve view,  $\times 124$ ; 6, paratype, SUGDMF no. 605, carapace, dorsal view,  $\times 100$ . 7, 8. *Xestoleberis subglobosa* (Bosquet). 7, carapace, SUGDMF no. 606, left valve view,  $\times 164$ ; 8, carapace, SUGDMF no. 607, dorsal view,  $\times 135$ . 9. *Paracypris khuialaensis* Bhandari, carapace, SUGDMF no. 608, right valve view,  $\times 71$ . 10–13. *Paracandona andhraensis* sp. nov. 10, holotype, SUGDMF no. 609, left valve, lateral view,  $\times 129$ ; 11, paratype I, SUGDMF no. 610, right valve, internal view,  $\times 131$ ; 12, paratype II, SUGDMF no. 611, left valve, internal view,  $\times 144$ ; 13, paratype III, SUGDMF no. 612, right valve, dorsal view,  $\times 151$ .

## Section I.

**Diagnosis.**—Surface marked by a prominent groove in posteroventral region, an arcuate carina near posterior margin in right valve, and broad shallow reticulation.

**Description.**—Carapace elongate, subquadrate in lateral view, with greatest height about half of length, at anterior cardinal angle; left valve larger than right valve, overlapping distinctly along anterior and posterodorsal margins; dorsal margin nearly straight; ventral margin sinuate; anterior margin broadly rounded; posterior margin subangulate near mid-height; in dorsal view carapace somewhat inflated, maximum width half of length posteriorly, anterior end narrow, posterior region laterally compressed. Eye tubercle distinct. Valve surface marked by a prominent groove in posteroventral region; a depression posterior to eye tubercle; arcuate carina near posterior margin in right valve; anterior marginal area compressed and smooth; rest of the area ornamented by broad shallow reticulations, arranged in concentric pattern. Inner lamella narrow; line of concrescence and inner margin coincide; selvage distinct near inner periphery; normal pores widely spaced. Hinge antimerodont; in right valve it comprises 8 anterior and 6 or 7 posterior terminal teeth and loculate median groove.

**Dimensions.**—Holotype, SUGDMF no. 594, a carapace, length 0.53 mm, height 0.26 mm, width 0.27 mm; paratype I, SUGDMF no. 595, a carapace, length 0.53 mm, height 0.26 mm, width 0.26 mm; paratype II, SUGDMF no. 596, a right valve, length 0.51 mm, height 0.26 mm.

**Discussion.**—The species was originally described as *Cytheridella* sp. by Bhandari (1995) from the Inter-trappean beds of Duddukuru. However, unlike the genus *Cytheridella*, which is characterised by an adont hinge, the new species has a distinct antimerodont hinge structure.

The present species resembles *Hapsicytheridea binodosa* Al-Furaih (1980) from the Lower Paleocene of Saudi Arabia in overall outline and surface ornamentation but differs in the absence of two nodes in the posterolateral region and other ornamental details. The species also lacks a clear caudal process along the posterior margin.

**Occurrence.**—Sections I and II.

Subfamily Cytherurinae  
Genus *Cytherura* Sars, 1866

**Type species.**—*Cythere gibba* O. F. Müller, 1785.

*Cytherura duddukuruensis* sp. nov.

Figure 4.11–4.13

**Etymology.**—After the village of Duddukuru.

**Material.**—309 carapaces.

**Type locality.**—Light yellow limestone (Sample SUGDMF no. 3/II), Inter-trappean beds, Paleocene.

## Section II.

**Diagnosis.**—Carapace pear-shaped in lateral outline; surface ornamented by dense fine punctation.

**Description.**—Sexual dimorphism distinct, males being more elongate, less high and less wide than females; carapace pear-shaped in lateral outline, with greatest height at anterior cardinal angle; valves strongly compressed posteroventrally; overlap indistinct; dorsal margin straight, converging posteriorly; ventral margin distinctly sinuate medially; anterior margin broad and obliquely rounded; posterior margin with a caudal process at mid-height; in dorsal view, carapace biconvex with maximum width near middle, ends compressed. Valve surface ornamented by dense, fine punctation. Internal characters not known.

**Dimensions.**—Holotype, SUGDMF no. 597, a female carapace, length 0.40 mm, height 0.24 mm, width 0.16 mm; paratype I, SUGDMF no. 598, a female carapace, length 0.40 mm, height 0.24 mm, width 0.18 mm; paratype II, SUGDMF no. 599, a male carapace, length 0.42 mm, height 0.21 mm, width 0.14 mm.

**Discussion.**—*Cytherura duddukuruensis* sp. nov. resembles *Cytherura interposita* Lyubimova and Guha in Lyubimova *et al.* (1960) from the Miocene of Kachchh in overall shape. The latter species, however, differs from the present species in having an oblong lateral outline, a shallow vertical sulcus and reticulation, and meshes enclosing two or more punctae.

**Occurrence.**—Sections I and II.

Genus *Semicytherura* Wagner, 1957

**Type species.**—*Cythere nigrescens* Baird, 1838.

*Semicytherura diluta* sp. nov.

Figure 5.2–5.4

**Etymology.**—From Latin *diluta* meaning weakened or thinned; with reference to the faint ornamentation.

**Material.**—110 carapaces.

**Type locality.**—Light yellow limestone (Sample SUGDMF no. 1/II), Inter-trappean beds, Paleocene. Section II.

**Diagnosis.**—Surface ornamented by feeble transverse ridges and reticulation in ventral half.

**Description.**—Sexual dimorphism distinct, males being more elongate, less high and more wide than females; carapace subovate in lateral outline, with greatest height near middle and greatest length below mid-height; overlap indistinct; dorsal margin strongly convex in females and arched in males; ventral margin concave anteriorly but convex posteriorly; anterior margin narrowly rounded; posterior drawn out in a caudal process slightly below mid-height; in dorsal view carapace biconvex, posterior end compressed,



maximum width near middle in females, posterior in males. Valve surface ornamented by feeble transverse ridges in ventral half, lowermost ridge continuous from anteroventral to posteroventral region, other ridges intersecting each other in ventromedian region forming weak reticulation; fine punctation over rest of area.

*Dimensions*.—Holotype, SUGDMF no. 601, a female carapace, length 0.42 mm, height 0.26 mm, width 0.22 mm; paratype I, SUGDMF no. 602, a male carapace, length 0.46 mm, height 0.24 mm, width 0.22 mm; paratype II, SUGDMF no. 603, a female carapace, length 0.43 mm, height 0.26 mm, width 0.22 mm.

*Discussion*.—*Semicytherura diluta* sp. nov. closely resembles *Semicytherura indica*? subspecies described by Neale and Singh (1985, pl. 46, fig. 2) in overall outline and ornamentation. *S. indica*? subspecies is based on a single specimen and inadequately described. It differs from *S. diluta* in having feeble transverse ridges all over the valve surface and a nearly straight ventral margin.

*Semicytherura longilinea* Bhandari (1995) from the Lower Eocene Khuiala Formation of Jaisalmer resembles *S. diluta* in appearance. However, it differs in having 9 or 10 transverse ridges that extend nearly the entire length of the carapace.

*Occurrence*.—Section II.

Family Xestoleberididae  
Genus *Uroleberis* Triebel, 1958

*Type species*.—*Eocytheropteron parnensis* Apostolescu, 1955.

*Uroleberis rasilis* sp. nov.

Figure 5.5, 5.6

*Etymology*.—From Latin *rasilis*, meaning smoothed; with reference to smooth surface.

*Material*.—Three carapaces.

*Type locality*.—Greyish-white limestone (Sample SUGDMF no. 7/II), Inter-trappean beds, Paleocene, Section II.

*Diagnosis*.—Carapace ovate in lateral outline; posterior margin with an indistinct caudal process.

*Description*.—Carapace ovate in lateral outline, with greatest height near middle; left valve slightly overlaps right valve along dorsal and posterior margins; dorsal margin arched; ventral margin nearly straight; anterior margin narrowly rounded; posterior margin slightly concave in upper part, rounded in lower part and with indistinct caudal process; in dorsal view carapace biconvex, ends narrowed, maximum width slightly posterior to middle. Valve surface smooth.

*Dimensions*.—Holotype, SUGDMF no. 604, a carapace,

length 0.45 mm, height 0.30 mm, width 0.30 mm; paratype, SUGDMF no. 605, a carapace, length 0.45 mm, height 0.32 mm, width 0.32 mm.

*Discussion*.—The species resembles *Uroleberis* sp. aff. *U. sp. 1* described by van den Bold (1988) from the Upper Miocene-Pliocene of the Dominican Republic in lateral outline but differs in the absence of transverse ridges in the ventral region.

*Occurrence*.—Section II.

Superfamily Cypridacea Baird, 1845  
Family Candonidae Kaufmann, 1900  
Subfamily Candoninae Kaufmann, 1900  
Genus *Paracandona* Hartwig, 1899

*Type species*.—*Candona euplectella* Brady and Norman, 1889.

*Paracandona andhraensis* sp. nov.

Figure 5.10–5.13

*Etymology*.—After the Indian state of Andhra Pradesh.

*Material*.—Ten valves.

*Type locality*.—Light yellow limestone (Sample SUGDMF no. 3/I), Inter-trappean beds, Paleocene, Section I.

*Diagnosis*.—Valve surface marked by dense reticulation, meshes enclosing 3 or 4 punctae.

*Description*.—Valve subrectangular in lateral outline, with greatest height a little over half of length near anterior cardinal angle; dorsal margin straight; ventral margin slightly concave anterior to middle; anterior margin broad and evenly rounded; posterior margin slightly narrow, sloping down in upper half and rounded in lower; posterior cardinal angle distinct; in dorsal view valve nearly convex, flat medially. Valve surface ornamented by dense reticulation, arranged concentrically, meshes enclosing 3 or 4 punctae; anterior and posteroventral regions laterally compressed. Inner lamella narrow; line of concrescence and inner margin coincide; selvage well developed, near inner periphery. Hinge modified adont; in right valve it consists of a smooth ridge, selvage at its terminal ends raised giving socketlike appearance; hinge complementary in left valve. Central muscle scars not known.

*Dimensions*.—Holotype, SUGDMF no. 609, a left valve, length 0.45 mm, height 0.24 mm; paratype I, SUGDMF no. 610, a right valve, length 0.45 mm, height 0.22 mm; paratype II, SUGDMF no. 611, a left valve, length 0.43 mm, height 0.22 mm; paratype III, SUGDMF no. 612, a right valve, length 0.42 mm, height 0.22 mm.

*Discussion*.—The species resembles *Paracandona* aff. *belgica* Tambareau, 1984, described from the Thanetian of the Paris Basin in subrectangular lateral outline and reticu-

lated ornamentation. *Paracandona* aff. *belgica*, unlike the present species, has fine, hexagonal reticules and lacks laterally compressed anterior and posteroventral margins.

*Occurrence.*—Section I.

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# Fossil crabs (Crustacea: Decapoda: Brachyura) from the latest Miocene Senhata Formation, Boso Peninsula, Japan

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**Abstract.** Two species of fossil decapods, *Maja tomidai* sp. nov. and *Daldorfia* sp. are described from the latest Miocene Senhata Formation of the Boso Peninsula, central Japan. The former species resembles *Maja morii* Kato from the middle Miocene of Japan and *Maja dominoleuae* Hu and Tao from the late Miocene of Taiwan. A large palm of *Daldorfia* sp. is the third fossil record of the genus from Japan. The discovery of *Daldorfia* sp. supports the existence of subtropical to tropical marine conditions in the latest Miocene of the Boso Peninsula indicated previously by molluscan evidence.

**Key words:** Brachyura, Crustacea, *Daldorfia*, Decapoda, *Maja*, Senhata Formation, Zushi Fauna

## Introduction

Decapod Crustacea from the upper Miocene of Japan have previously been reported from the Tano and Aya formations of the Miyazaki Group, Kyushu (4 species; Karasawa, 1993, 1997; Karasawa and Kato, 1996); the Uchiumigawa Group, Kyushu (1 species; Karasawa, 1990); the Itahana Formation of the Tomioka Group, central Japan (8 species; Kato, 2001); the Aose Formation, north of Sendai (1 species; Karasawa and Kato, 1996), and the Wakkanai Formation, Hokkaido (1 species; Imaizumi, 1952).

Two species of decapod crustaceans were obtained from exposures of the upper Miocene Senhata Formation in the Matsukura Kogyo Quarry in Motona, Kyonan Town, Chiba Prefecture (35° 9' N, 135° 51' E) (Figure 1). A specimen found by S. Tomida represents a new species of the majid genus *Maja*. Several additional fragmentary specimens were subsequently collected from the same locality by N. Kaneko and donated to the Natural History Museum and Institute, Chiba. The other specimen collected by K. Usui is identified as a large palm belonging to the daldorfiid genus *Daldorfia*.

The purpose of this paper is to describe the new species of *Maja* and the undetermined species of *Daldorfia*, and to discuss their phylogenetic and paleobiogeographic implications. The material described herein is deposited in the Mizunami Fossil Museum (MFM) and Natural History

Museum and Institute, Chiba (CBM-PI).

## Locality and paleoenvironments

The Senhata Formation exposed at the present locality is up to 130 m in thickness and is composed mainly of coarse-grained sediments, intercalating mudstones and pyroclastics (Yabe and Hirayama, 1998). The formation yields abundant remains of marine animals such as molluscs, hermatypic corals, bryozoans, isopods, echinoids, elasmobranchs and mammals.

The geologic age of the Senhata Formation has been discussed from various viewpoints. Ibaraki and Tsuchi (1980) assigned the formation to Blow's (1969) planktonic foraminifera Zone N17. Kanie *et al.* (1991) reported calcareous nannofossils indicative of the CN9 Zone of Okada and Bukry (1980) from the underlying Amatsu Formation and the CN10b Zone from the overlying Inakozawa Formation. Kasuya (1987) reported a fission-track age of  $6.3 \pm 0.4$  Ma for the Ok tuff bed in the lower part of the Inakozawa Formation. To sum up these data, the geologic age of the Senhata Formation is regarded as the latest Miocene.

O'Hara and Ito (1980) studied the molluscs of the Senhata Formation and noted that the assemblage is a mixture of relatively worn and fragmented shells of shallow-water inhabitants and well preserved shells of deep-water dwellers. They concluded that the shallow-water

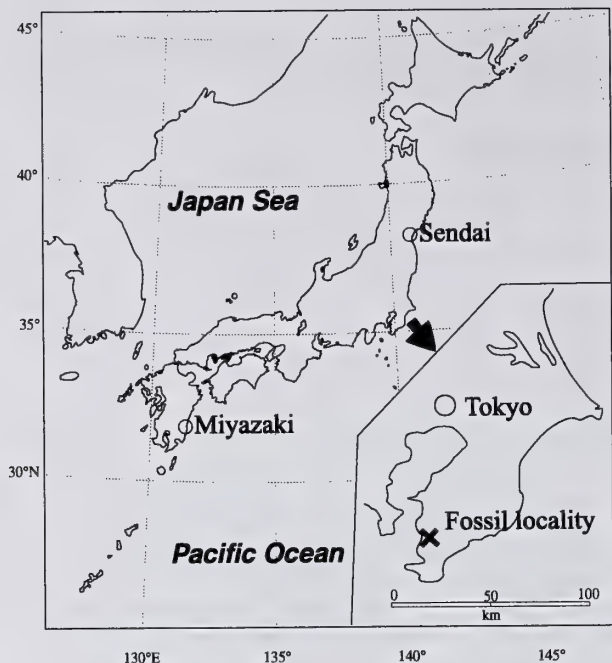


Figure 1. Map showing the fossil locality.

assemblage was mixed with a bathyal assemblage as a result of short distance transportation by bottom currents. Tomida (1989, 1996) recognized seven types of molluscan assemblages in the formation. He also considered the molluscan assemblage of the present locality to be a mixture of both a bathyal assemblage (200–250 m in depth on the continental slope) and mesoneritic to subneritic assemblages that were transported from shallower waters. Based on the occurrences of the isopod *Palaega*, Karasawa *et al.* (1992) suggested an upper bathyal paleoenvironment for the Senhata Formation.

Tomida and Itoigawa (1986) and Tomida (1989) reported the occurrences of the planktonic gastropod *Hartungia* sp. and cephalopods such as *Aturia* and *Argonauta* in various growth stages from the present locality. Based on the presence of these characteristic genera and other subtropical to tropical molluscs, Tomida (1983, 1996), Tomida and Itoigawa (1986) and Ozawa and Tomida (1992, 1996) deduced that the Senhata Formation was deposited under the influence of warm-water currents. In their study of the selachian (shark) assemblage of the Senhata Formation, Yabe and Hirayama (1998) also concluded that this formation was deposited in the upper part of the continental slope under the influence of warm-water currents.

Ozawa and Tomida (1992) and Ozawa *et al.* (1995) proposed the term “Zushi Fauna” for some late Miocene to early Pliocene molluscan assemblages on the Pacific side of Japan which contain molluscan species indicative of tropi-

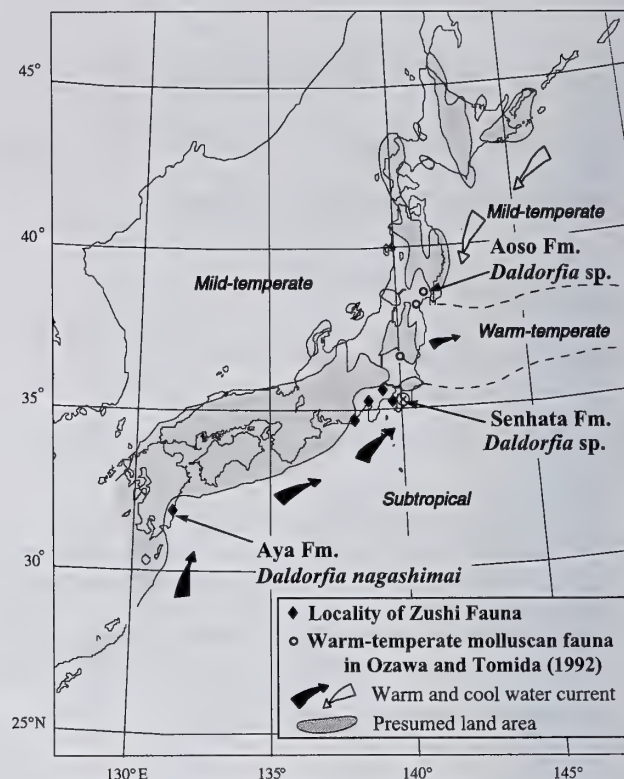


Figure 2. Localities of fossil *Daldorfia* species. Distribution of the Zushi Fauna and reconstruction of paleogeography are modified after Ozawa and Tomida (1992), Ogasawara (1994) and Nakamura *et al.* (1999). The paleoclimatology is based on Ogasawara's (1994) divisions.

cal to subtropical marine climates (Figure 2). They correlated this warmer marine climate with “Climatic Optimum 3” of Barron and Baldauf (1990).

Among the decapod genera here described, the genus *Maja* has 16 living species, of which 13 occur in the Indo-West Pacific (Griffin and Tranter, 1986) and 7 in Japanese warm-temperate to tropical waters south of the Boso Peninsula, central Japan (Sakai, 1976). The genus *Daldorfia* includes 6 living species in tropical to subtropical Japanese waters (Sakai, 1976). Particularly, *D. horrida* (Linnaeus, 1758), the most closely related to *D. sp.* from the Senhata Formation, inhabits tropical to subtropical waters south of the Kii Peninsula in Japan, the area washed by the warm Kuroshio Current (Sakai, 1976). Judging from the distributions of living species, the decapod species found in the Senhata Formation support the view previously suggested by molluscan evidence that a warm marine climate existed along the Pacific coast of Japan in the latest Miocene.

Fossil species of *Daldorfia* have hitherto been recorded from the upper Miocene of Japan and Oligocene of North America. They are *D. nagashimai* Karasawa and Kato,



1996 from the Aya Formation, Miyazaki Group in southwest Japan, *Daldorfia* sp. from the Aoso Formation in northeast Japan (Karasawa and Kato, 1996; Figure 2), and *Daldorfia himaleorhaphis* Schweitzer, 2001a from the Jansen Creek Member of the Makah Formation in the Olympic Peninsula, Washington State, the United States of America.

The Aya Formation yields molluscan species typical of the "Zushi Fauna" (Nakamura *et al.*, 1999). While Ozawa and Tomida (1992) suggested that the "Zushi Fauna" extended north into the Fukuda Formation, south of Sendai, the occurrence of *Daldorfia* sp. from the Aoso Formation indicates that the fauna extended north of Sendai, where a warm-water event is suggested by molluscs (Ogasawara, 1994) and planktonic foraminiferal assemblages correlative with "Climatic Optimum 3" of Barron and Baldauf (1990) (Saito and Isawa, 1995). The occurrences of *Daldorfia* spp. from the Aya, Senhata and Aoso formations provide additional biotic evidence for the warming event in the late Miocene to early Pliocene in northeast Japan. The occurrence of the oldest known species of *Daldorfia*, *D. himaleorhaphis* from the Oligocene of Washington State, is considerably distant geographically from the distribution of living species of this genus. However, the high diversity of the decapod assemblages, including subtropical species from the Eocene to Oligocene of the Pacific North America, indicates a much warmer marine climate in this area than prevails today (Schweitzer, 2001b).

### Systematic descriptions

Section Heterotremata Guinot, 1977  
Superfamily Majoidea Samouelle, 1819  
Family Majidae Samouelle, 1819  
Subfamily Majinae Samouelle, 1819  
Genus *Maja* Lamarck, 1801

*Type species.*—*Cancer squinado* Herbst, 1788. By subsequent designation (ICZN opinion 511).

*Discussion.*—Based upon larval morphology, Rice (1983) proposed a phylogenetic relationship between genera within the family Majidae, regarding *Maja* as a "primitive" and *Leptomithrax* as an "advanced" form. Several previous studies also supposed the same relationship between the two genera (e.g. Kurata, 1969). The cup-shaped orbit of living species of *Leptomithrax* (three closely spaced orbital spines and the antennal fossa excluded from the orbit) is generally regarded as more "complete" than that of *Maja* (separate spines with an antenna included within the orbit). However, the orbital features of the early middle Miocene *Maja morii* Kato, 1996 from Japan resemble those of *Leptomithrax*, including its postorbital spine which exhibits an excavated anterior surface like that

typically observed in *Leptomithrax* (Griffin, 1966).

With respect to the posterior end of the carapace, the Japanese fossil *Maja* species, *M. morii* and the new species discussed herein have a single tubercle on the posterior end of the carapace as in *Leptomithrax longipes* (Thomson, 1902), a living species found in Australia and New Zealand. In its adult and larval morphologies, *L. longipes* was regarded as unique among the members of the genus *Leptomithrax* (Webber and Wear, 1981; McLay *et al.*, 1995).

Judging from these characters the phylogenetic relationship between *Leptomithrax* and *Maja* should be reconsidered. The oldest fossil record of *Maja* is from the early Miocene (*Maja robinsoni* Jenkins, 1985 from South Australia), while that of *Leptomithrax* extends into the late Eocene (*Leptomithrax griffini* Feldmann and Maxwell, 1990 from New Zealand), suggesting that *Maja* is a more advanced form than *Leptomithrax*.

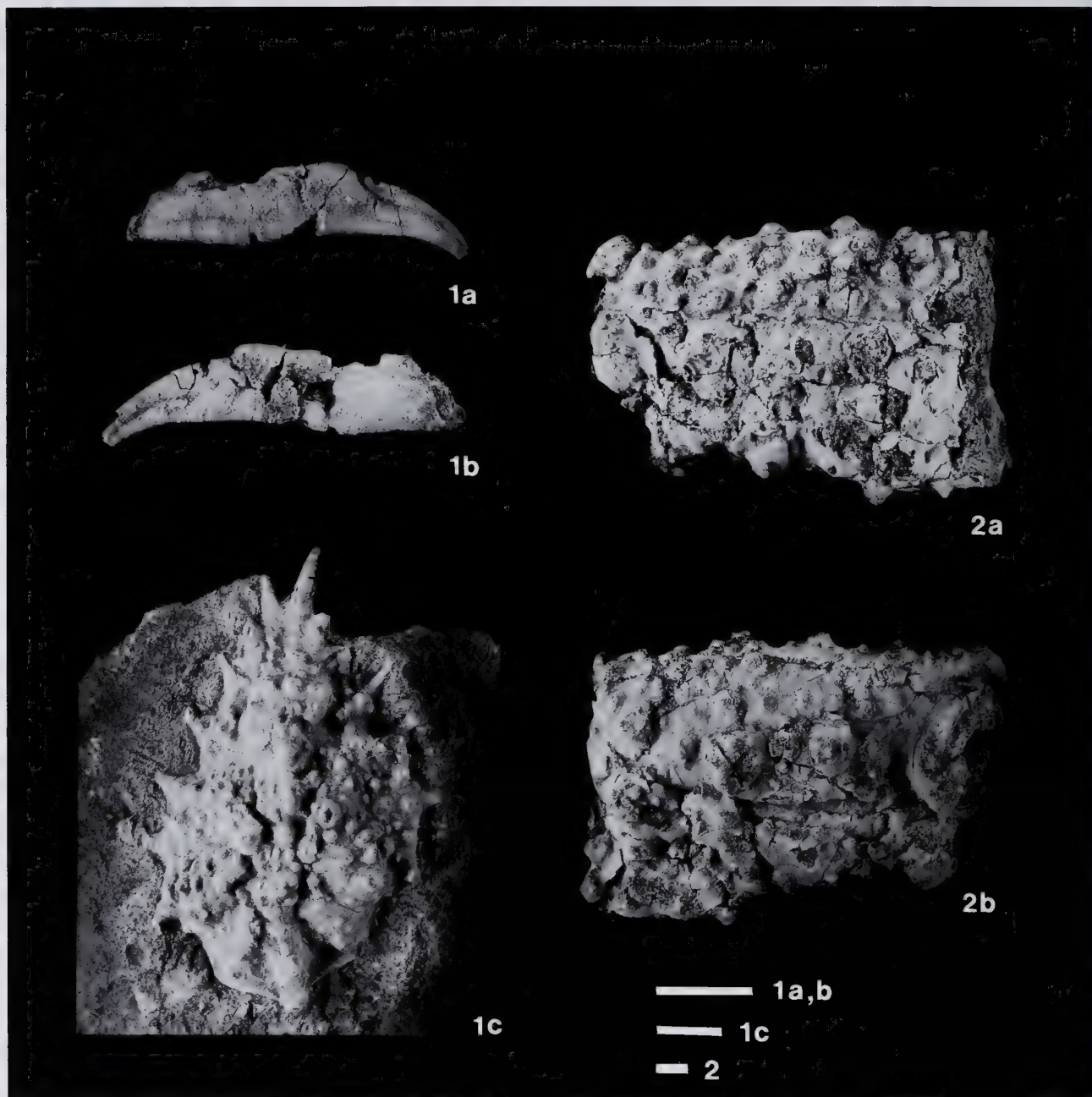
*Geologic range.*—Miocene to Recent.

### *Maja tomidai* sp. nov.

Figures 3.1a–c, 4, 5B

*Diagnosis.*—*Maja* with moderately long, divergent rostrum; lateral and dorsal spines acute. Intercalated and postorbital spines approximated. Dorsal regions densely covered with large, conical tubercles. Posterior end of carapace bearing single conical tubercle.

*Description.*—Carapace pyriform in outline. Rostrum bifid, acute, widely divergent anterolaterally. Orbit rounded. Supraorbital cave thick, sparsely granulate. Antorbital spine acutely triangular, directed laterally, slightly curved posteriorly. Intercalated spine short, triangular, about half length of antorbital and one-third length of postorbital spines. Postorbital spine triangular, directed anteriorly. Intercalated and postorbital spines closely approximated. Basal antennal article directed forward with anteromedial and anterolateral spines. Anterolateral margin of carapace bears acute, long hepatic spine and three acute branchial spines; posteriormost one lies dorsally. Dorsal regions well defined. Gastric, branchial, and hepatic regions strongly convex, covered with pointed, variable-sized conical tubercles. Frontal region with two longitudinal series of conical tubercles; tubercles extending to base of rostrum, increasing in size posteriorly. Mesogastric region strongly convex with two large, conical tubercles arranged longitudinally. Metagastric region also highly convex with large median tubercle. Urogastric region with conical tubercle markedly smaller than others. Cardiac region strongly convex, defined laterally by broad, plain furrows, and medially by a large, conical tubercle. Intestinal region elevated, forming acute spine. Hepatic region with clustered tubercles, bordered by broad, plain depressions. Branchial re-



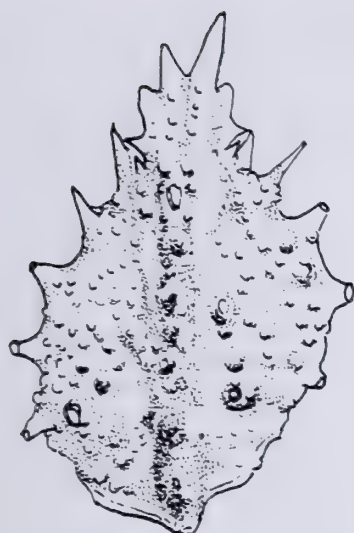
**Figure 3.** 1. *Maja tomidai* sp. nov., MFM 83053. Holotype. a and b, outer and medial surface of the right chela,  $\times 1.5$ ; c, carapace,  $\times 1.0$ . 2. *Daldorfia* sp., CBM-PI 01084, manus of right chela; a ; outer surface, b ; medial surface. CBM-PI 01084,  $\times 0.5$ . Scale bars = 10 mm.

gions with numerous variable-sized tubercles. Sinuous swellings extending parallel to branchiocardiac groove consisting of large tubercles. Metabranial region convex with sparse tubercles and granules, less developed than mesobranial and intestinal swellings. Posterolateral margin rimmed, sinuously convex. Posterior end of carapace bearing one large, conical, axial tubercle. Palm of right cheliped slightly curved upward; preserved part of

outer surface smooth. Fingers acute, slender, obviously curved downward.

**Discussion.**—In carapace outline, the present species most resembles *Maja dominoleuae* Hu and Tao, 1985 from the upper Miocene of Taiwan. However, *M. tomidai* sp. nov. is easily distinguished from *M. dominoleuae* in that the orbital spines are shorter and slightly curved upward, and the dorsal surface of the carapace is densely covered by





**Figure 4.** Line drawing showing the dorsal view of carapace of *Maja tomidai* sp. nov. The specimen is compressed obliquely, causing the right half of the carapace to be displaced anteriorly. Scale bar = 10 mm.

large tubercles. *Maja tomidai* sp. nov. resembles *M. morii* Kato, 1996 from the early middle Miocene of the Chichibumachi and Takaku groups, Saitama and Fukushima prefectures, Japan (Kato and Karasawa, 1995) in the general arrangement of tubercles and lateral spines of the carapace, but differs in having denser tubercles and more elongated spines on the dorsal surface. In addition, the antennal fossa of *Maja morii* seems to lie outside the orbit, while that of *Maja tomidai* is included within the orbit like living species of *Maja* (Figure 5).

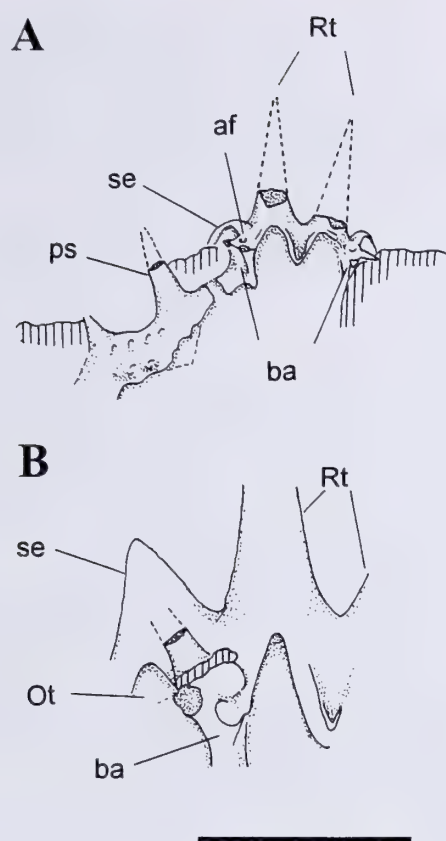
Despite these differences, *M. tomidai* sp. nov. shares the following important characters with *M. morii*: (1) the three orbital spines are relatively approximated, and (2) the posterior end of the carapace has a single conical tubercle. Most living species of *Maja* possess a pair of spines or tubercles on the posterior end of the carapace, and no species in this genus has a large, single tubercle on the posterior end of the carapace like *M. tomidai* sp. nov. and *M. morii*. Due to the incompleteness of known specimens, unfortunately, the ventral orbital features and the posterior end of the carapace of *M. dominoleuae* are not available.

The carapace of the holotype is compressed and severely deformed (Figure 4).

**Material examined.**—MFM 83053 (Holotype: carapace and appendages). CBM-PI 01085-01087.

**Etymology.**—Named after Susumu Tomida who contributed greatly to the paleontology of the Senhata Formation and discovered the holotype specimen.

**Measurements.**—Holotype, maximum carapace length



**Figure 5.** Line drawing showing the ventral orbital features of (A) *Maja morii* Kato, 1996 (CBM-PI 00177, Numanouchi Formation, Takaku Group) and (B) *Maja tomidai* sp. nov. (holotype). Abbreviations: **Ot**, orbit, **Rt**, rostrum, **af**, antennal fossa, **ba**, basal antennal article, **ps**, postorbital spine, **se**, supraorbital eave. Scale bar = 10 mm.

(including rostrum), 78.0 mm; maximum carapace width (excluding the branchial spines), 43.5 mm. Palm length, 37.0 mm.

Superfamily Parthenopoidea MacLeay, 1838  
Family Daldorfiidae Ng and Rodriguez, 1986  
Genus *Daldorfia* Rathbun, 1904

**Type species.**—*Cancer horridus* Linnaeus, 1758. By monotypy.

**Geologic range.**—Oligocene to Recent.

#### *Daldorfia* sp.

Figure 3.2a, b

**Description.**—Manus of right cheliped without fixed finger large (length, 131 mm), strongly compressed; upper and lower margins diverging distally. Lateral and medial surfaces densely nodose. Nodes conical to irregular; variable

in size up to 20 mm in diameter; surface bearing clusters of various-sized tubercles. Furrows between nodes shallow, smooth except for scattered small conical tubercles. Superior socket of articulation, situated near dorsoproximal corner of manus and directed proximally. Proximal margins of lateral and medial surfaces bearing rounded, thick rims along articulation with carpus.

**Discussion.**—The previously known fossil record of this genus from Japan includes *Daldorfia nagashimai* Karasawa and Kato, 1996 from the latest Miocene Aya Formation, Miyazaki Group in southwest Japan and *D. sp.* from the late Miocene Aoso Formation to the north of Sendai in northeast Japan (Karasawa and Kato, 1996) (Figure 2). *Daldorfia?* sp. from the middle Miocene Aoki Formation in central Japan (Karasawa *et al.*, 1999) is too incomplete to permit generic assignment. It may belong to a species of the Majidae. Therefore, *Daldorfia* sp. described here is the third fossil record for this genus from Japan.

Living species of *Daldorfia* are inhabitants of littoral and sublittoral zones (Sakai, 1976). Judging from the disarticulated and incomplete state of the present specimen, it may have been transported from a littoral or sublittoral zone, together with shallow-water molluscs, to the deeper-water environment of the Senhata Formation.

**Material examined.**—CBM-PI 01084.

**Measurements.**—Manus length, 131 mm, manus height, 88 mm.

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# Internal test morphology of the genus *Rectobolivina* (Cushman, 1927) from the Late Cenozoic Miyazaki Group, southwestern Japan

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**Abstract.** Six species of the genus *Rectobolivina* (benthic foraminifera), *R. asanoi*, *R. bifrons*, *R. clavata*, *R. discontinuosa*, *R. raphana* and *R. striatula* from the Late Cenozoic Miyazaki Group of southwestern Japan were taxonomically studied, particularly focusing on internal test morphology. Two new species of *Rectobolivina*, *R. clavata* and *R. discontinuosa*, and one new replacement name, *Rectobolivina clavatostriatula*, are proposed. Scanning electron microscopic and optical microscopic observations of dissected specimens and thin sections reveal that the chamber wall of the genus *Rectobolivina* is bilamellar, and that the toothplate is an extension of the chamber wall, a twisted plate strongly folded at both edges and connecting successive foramina. The toothplate constantly attaches with one of its sides to the axial side of the inner margin of the preceding foramen. It exhibits a lamellar structure, showing that the extension of the outer lamella of the chamber wall is covered by two thin inner lamellae on both axial and peripheral sides.

The six species of *Rectobolivina* display a clear stratigraphically separated distribution during the period from latest Miocene to earliest Pleistocene.

**Key words:** benthic foraminifera, internal morphology, lamellar structure, Miyazaki Group, *Rectobolivina*, toothplate

## Introduction

The current classification scheme of benthic foraminifera requires examination of the internal test morphology (Loeblich and Tappan, 1987). This is mainly caused by the development of scanning electron microscopy (SEM) since the 1960's and of techniques for dissecting specimens.

The genus *Rectobolivina* proposed by Cushman (1927) differs from the genus *Siphogenerina* Schlumberger, 1882 by its biserial chamber arrangement in the earlier stage, in contrast to the triserial one in *Siphogenerina*. Hofker (1951a) indicated the importance of the toothplate of *Rectobolivina* at generic level, and Hofker (1951b) pointed out the difference of toothplate orientation between *Rectobolivina* and *Siphogenerina*. The current classification (Loeblich and Tappan, 1964, 1987) adopted the significance of the toothplate orientation. Although Revets (1993) briefly described the monolamellar structure in the toothplate of the genus *Siphogenerinoides* Cushman, 1927,

which shows the same toothplate orientation as *Rectobolivina*, the structure of the toothplate in *Rectobolivina* has not yet been described.

The present paper deals with the taxonomy of *Rectobolivina* species from the Late Cenozoic Miyazaki Group, with emphasis on the nature of the toothplate.

## Geologic settings

On the coastal region of Miyazaki Prefecture, southeast Kyushu, Late Cenozoic marine deposits named the Miyazaki Group are widely distributed. The Miyazaki Group unconformably overlies the Paleogene unit of the Shimanto Supergroup. Shuto (1952) divided the Miyazaki Group into three facies, the Aoshima, the Miyazaki, and the Tsuma facies from south to north, based on lithological differences and on their geographic distribution. The relationship among these facies has been thought to be contemporaneous. Shuto (1952) divided the Tsuma facies into three members, the Kawabaru, the Tsuma, and the

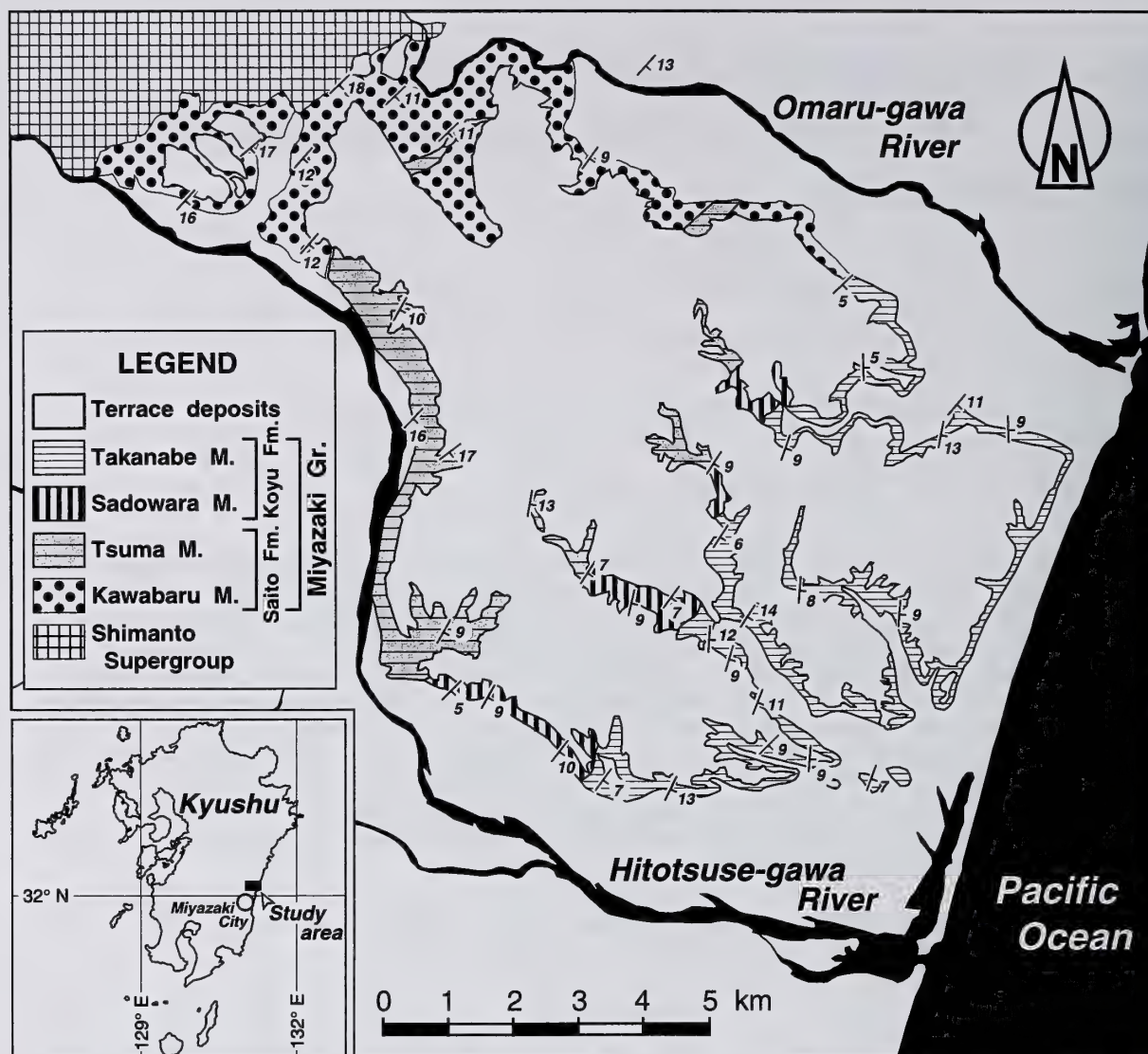


Figure 1. Geologic map of the study area (modified after Suzuki, 1987).

Takanabe Member in ascending order. The Tsuma facies was reclassified and subdivided into four members by Suzuki (1987) as follows: the Kawabaru and Tsuma Members of the Saito Formation, and the Sadowara and Takanabe Members of the Koyu Formation in stratigraphic order (Figure 1). The geologic age of the group was previously assigned to latest Miocene to earliest Pleistocene based on planktonic foraminifera by Natori *et al.* (1972) and calcareous nannoplankton by Nishida (1980).

The Tsuma facies is well exposed at the terrace cliffs along the Hitotsuse-gawa River. We collected 59 sediment samples for this study from this section (Figure 2).

## Materials and methods

Lithology and horizons of foraminifera-bearing rock samples in the section along the Hitotsuse-gawa River are shown in Figure 3. The pelitic layers in a siltstone/sandstone alternation were selected for sampling. Rock samples were disintegrated with an oversaturated sodium sulfate ( $\text{Na}_2\text{SO}_4$ ) solution following the method of Ujiie *et al.* (1977) and were washed using a 74  $\mu\text{m}$  sieve.

*Rectobolivina* specimens were picked out from the sediment residue on the sieve and identified with optical and scanning electron microscopes (SEM). A number of megalospheric specimens were dissected and observed under SEM following Nomura's (1983) Canada balsam-



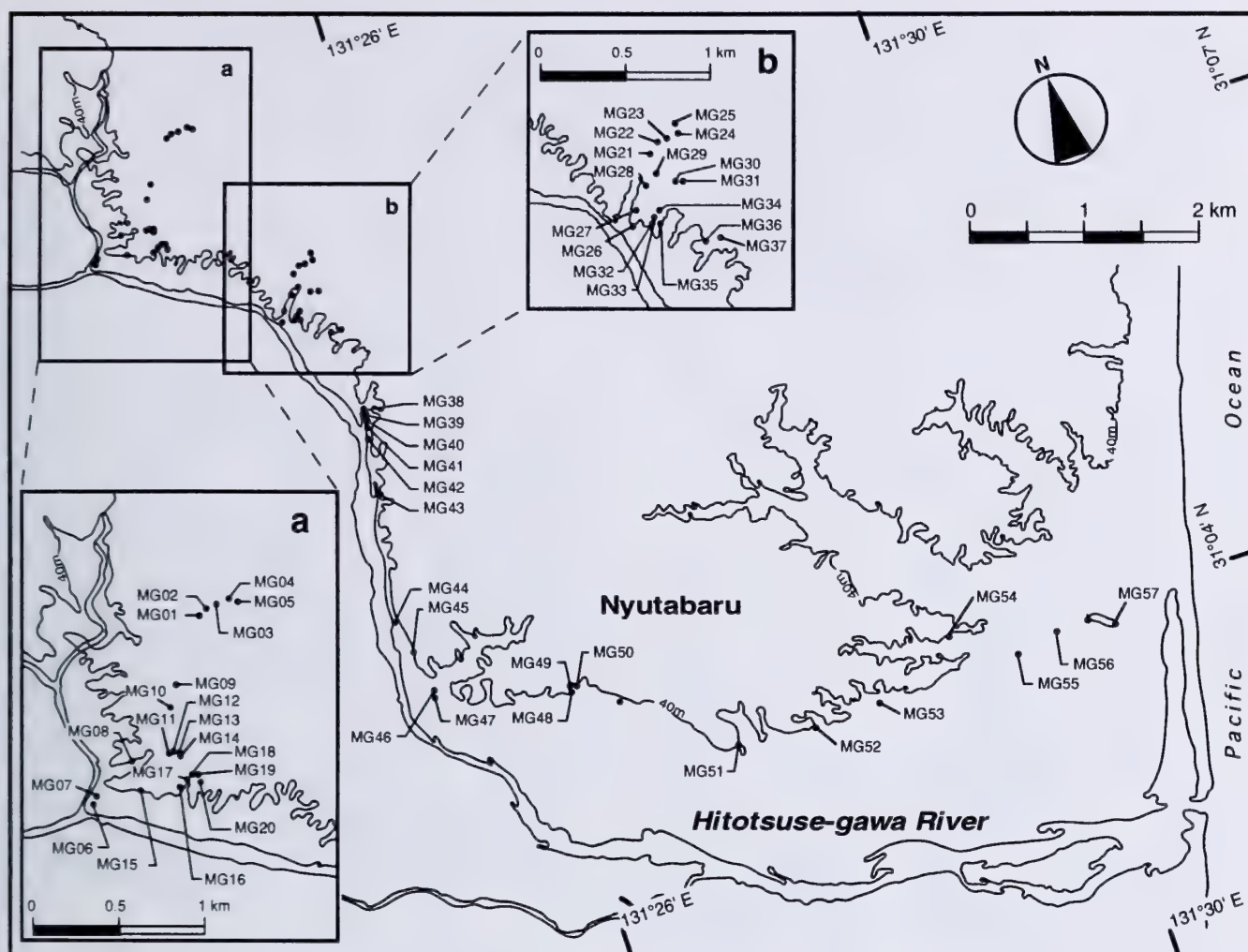


Figure 2. Map showing sampling localities.

xylene embedding method to examine the internal test structures.

All the illustrated specimens are deposited in the collections of the University of Tsukuba with catalog number prefixed IGUT.

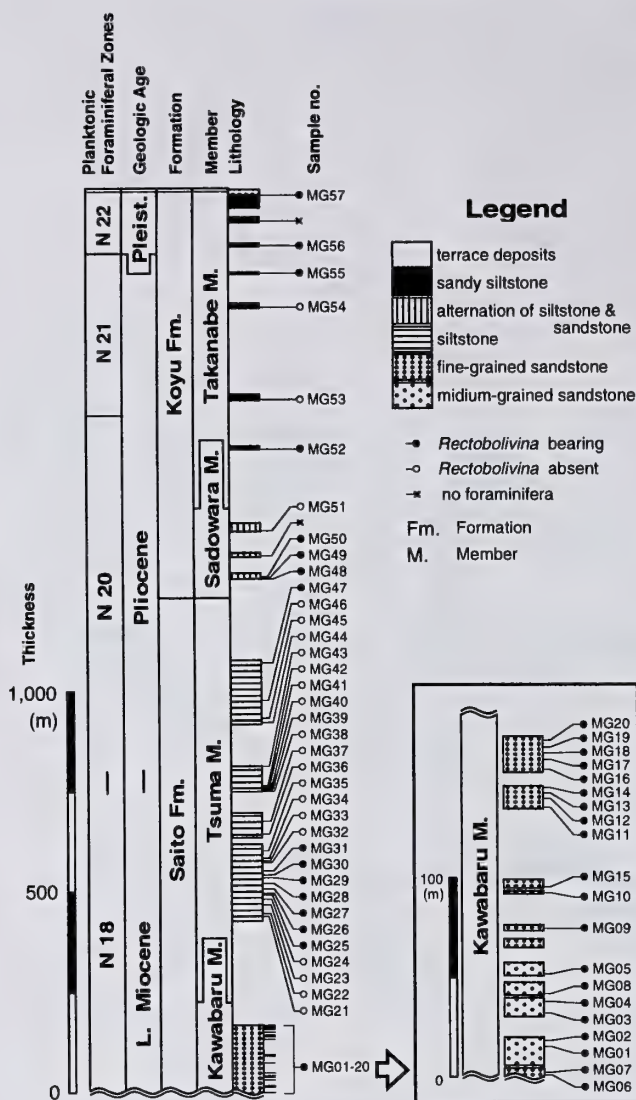
#### Brief note on stratigraphic occurrence

*Rectobolivina asanoi* Murata, 1951, *R. bifrons* (Brady, 1881), *R. clavata* sp. nov., *R. discontinuosa* sp. nov., *R. raphana* (Parker and Jones, 1865), and *R. striatula* (Cushman, 1913) were recognized in 35 sampling horizons (Figure 4). As shown in Figure 5, the stratigraphic distribution and the frequency of occurrence of these species are different in the study section. *R. asanoi* characteristically occurs only in the Kawabaru Member of uppermost Miocene age. *R. bifrons* and *R. striatula* occur at two ho-

rizons in the upper part of the Kawabaru Member and in the lower part of the Tsuma Member, while *R. clavata* sp. nov. is characteristic at two horizons, one in the upper part of the Tsuma Member and another in the lower part of the Sadowara Member. *R. raphana* occurs in the Takanabe Member. *R. discontinuosa* sp. nov. is restricted to the lowest Pleistocene horizon of the Takanabe Member. Possibly, these stratigraphic distributions of the species may offer clues for the restricted but detailed correlation of strata in a further study.

#### Previous studies on toothplate of *Rectobolivina*

Although Brady (1881, 1884) did not mention the existence of the toothplate in the original description of *Sagrina bifrons* (type species of *Rectobolivina*), Cushman (1913) described "the internal tubular connection" of *R. bifrons*



**Figure 3.** Geologic columnar section with the sampling levels. Stratigraphic division and thickness calculation are based on Suzuki (1987), and geologic age and planktonic foraminiferal zones are after Natori *et al.* (1972).

(his *Siphogenerina bifrons*) based on observations by optical microscopy. Cushman (1927, 1937) described the toothplate as "tube" or "tubular", and Hofker (1933) called it an "internal tube". Later, Hofker (1951a) examined toothplates of foraminifera including *Rectobolivina* species, and stated, "...in the biserial part of *Rectobolivina*, this plate is fastened at one side of the aperture of the former chamber, and is erected in such way, that, by contorting itself, it is attached to the opposite side of the chamber itself, giving rise to a tooth by means of its folded and flaring side...". He (fig. 35) illustrated in detail the schematic succession of toothplates in relation to the chamber arrangement for some

*Rectobolivina* species, particularly for *Rectobolivina columellaris* (Brady). He first showed that the toothplate of the genus is not a cylindrical tube but is a hemi-cylindrical plate. Hofker (1951b) showed the different modes of toothplate orientation in *Rectobolivina* and its related genus *Siphogenerina*; the angle between successive toothplates in *Rectobolivina* is constantly 180°, whereas it is 120° in *Siphogenerina*. Thus, the morphology and succession of the toothplates are now regarded as important taxonomic features. Loeblich and Tappan (1964) adopted Hofker's (1951b) opinion in their classification scheme of foraminifera and placed *Rectobolivina* into the family Bolivinitidae Cushman, 1927. They used the term "toothplate" only for the superfamily Buliminioidea (= their Buliminacea). Later, Loeblich and Tappan (1987) moved *Rectobolivina* into the subfamily Siphogenerinoidinae Saidova, 1981. The Siphogenerinoidinae consists of 11 genera, including *Rectobolivina* but not *Siphogenerina*, which are characterized by biserial chamber arrangement in earlier stage becoming uniserial in later stage, associated with the toothplate rotating 180° between chambers. Loeblich and Tappan (1987) defined the toothplate as an extension of the chamber wall and a contorted plate extending within the chamber lumen. Recently, Revets (1989, 1993, 1996) pointed out that the toothplate of the Buliminioidea (= his Buliminacea) (including *Rectobolivina*) originated from the inner layer of a bilamellar chamber wall, and he distinguished it from the so-called "toothplate" in the Rotalioidea, which shows a more complicated structure.

### Toothplate in *Rectobolivina*

Megalospheric specimens were vertically sectioned in two ways (Figure 6); i.e. cut through the broader diameter of test (Section A) and perpendicularly (section B).

The following description can be applied to all species treated here. The relationship among toothplate, foramen and chamber lumen is schematically shown in Figure 7.

The aperture of *Rectobolivina* species is elliptical to circular in outline and its top fuses to the apertural lip, which never distinctly protrudes (Figure 4). The toothplate is apparently thin and trough-shaped, strongly folded at its side edges as seen in section A (e.g. Figures 8.2, 11.7). The plate in the uniserial stage descends straight into the chamber lumen towards the preceding foramen, along the center of the test (e.g. Figure 10.5), whereas it extends in a zigzag way in the biserial stage, according to the biserial chamber arrangement (e.g. Figure 10.5). The trough-shaped concavity (tc) of the toothplate appears alternately from chamber to chamber in both biserial and uniserial stages (e.g. Figure 8.2). This indicates that the toothplate retains the early ontogenic biserial (= 180°) rotation, although cham-



bers become uniserial.

After slight etching with dilute hydrochloric acid solution, the chamber wall of *R. bifrons* (type species of the genus) shows a lamellar structure (Figure 8.5). The later chamber wall entirely covers the preceding ones, causing the thickening of the test wall in the earlier portion. The final chamber wall of *R. raphana* (Figure 11.4) is bilamellar, consisting of a thin inner lamella (il) and a thick outer lamella (ol). A similar lamellar structure can be seen in the toothplate (tp) of *R. bifrons* (Figure 9.2, 9.3), where a thick outer lamella (ol) is covered by a thin inner lamella (il) at both the axial and peripheral sides. In conclusion, it can be stated that the lamellae of the toothplate do not originate in the preceding toothplate nor septal wall, but represent an extension of the chamber wall (Figures 8.1, 9.2, 9.3, 9.5, 9.6). These observations on the lamellar structure of the toothplate differ from those by Revets (1989, 1993), who regarded the toothplate as an extension of the inner lining (= inner lamella in this study) of the chamber wall.

Our observation of the internal, lamellar structure in the genus *Rectobolivina* is summarized in Figure 12, and supports Hofker's (1951a) idea that the toothplate is a part of the chamber wall.

### Systematic description

Family Siphogenerinoidae Saidova, 1981

Subfamily Siphogenerinoidinae Saidova, 1981

Genus *Rectobolivina* Cushman, 1927

*Rectobolivina asanoi* Murata, 1951

Figures 4.1a-c, 4.2a-c; 10.1, 10.2; 13.1a, b

*Rectobolivina asanoi* Murata, 1951, p. 96, pl. 1, text-figs. 2a, b; Asano, 1952, p. 13, figs. 70, 71; Kawagata, 2001, p. 88, figs. 8-13a, b.

*Rectobolivina bifrons striatula* (Cushman) (non *Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917). Asano, 1950, p. 12, figs. 48, 49; Matsunaga, 1963, pl. 41, figs. 9a, b.

**Material.**—IGUT14488, sample MK07 (Figure 4.1a-c); IGUT14489, sample MK07 (Figure 4.2a-c); IGUT14490, sample MK07 (Figure 10.1); IGUT14491, sample MK07 (Figure 10.2).

**Remarks.**—Since Murata (1951) described *Rectobolivina asanoi* from the Miocene part of the Miyazaki Group, this species has been reported only from the late Neogene Shimajiri Group in Kume-jima Island, southwestern Japan (Kawagata, 2001). Comparing the original figure of *R. asanoi* Murata, 1951 (Figure 11.1a) to other costate *Rectobolivina* species, the former species is characterized in having a much wider test, and being elliptically rounded

in cross section. *R. bifrons* var. *striatula* (Cushman, 1917) of Suzuki (1987) from the lower part of the Miyazaki Group, south of the present study area, of Asano (1950) from the Pliocene Kakegawa Group, central Japan, and of Matsunaga (1963) from the Pliocene in Niigata Prefecture, northeastern Japan, are all probably identical to *R. asanoi*. The specimens treated here resemble those described as *R. striatula* (Cushman, 1917) from the late Neogene of New Zealand (Hornibrook, 1968; Hayward and Buzas, 1979) and from the Miocene of Victoria, Australia (Carter, 1964), and those described as *R. striatula* (Cushman, 1913) of Kennett (1966) from the late Neogene of New Zealand. However, these Southern Ocean species show cylindrical tests with numerous fine longitudinal striations (Carter, 1964; Kennett, 1966) or with fewer costae (Hornibrook, 1968; Hayward and Buzas, 1979), in contrast to the rather compressed test with a number of raised longitudinal costae in *R. asanoi*.

The megalospheric form of *R. asanoi* shows a bluntly rounded initial end and approximately four to five pairs of chambers in the biserial stage (Figure 4.1a, c), whereas the microspheric form has a rather tapered initial end and more chamber pairs in the earlier stage (Figure 4.2a, c). There is no distinct size difference between the forms.

### *Rectobolivina bifrons* (Brady, 1881)

Figures 4.3a-c, 4.4a-c; 8.2-8.5; 9.1-9.6; 13.2-13.4b

*Sagrina bifrons* Brady, 1881, p. 64; Brady, 1884, p. 582, pl. 75, figs. 18-20.

*Siphogenerina bifrons* (Brady). Cushman, 1913, p. 103, pl. 45, figs. 1a-2, 5-7; Cushman, 1921, p. 277, pl. 56, figs. 2, 3; Cushman, 1926, p. 16, pl. 3, figs. 7-9, pl. 4, fig. 4.

*Rectobolivina bifrons* (Brady). Cushman, 1927, p. 68, pl. 14, fig. 11; Cushman, 1937, p. 204, pl. 23, figs. 13, 14a, b; Asano, 1938, p. 606, pl. 16, figs. 11a, b; Asano, 1950, p. 11, figs. 46, 47; Asano, 1958, p. 28, pl. 5, figs. 10, 11; Kuwano, 1962, pl. 21, fig. 6; Huang, 1964, pl. 2, fig. 28; Ishiwada, 1964, pl. 4, fig. 68; Kikuchi, 1964, pl. 3, fig. 23; Belford, 1966, p. 45, pl. 9, figs. 13, 14; Inoue, 1989, pl. 28, fig. 6.

? *Siphogenerina* (*Sagrina*) *bifrons* (Brady). Egger, 1893, p. 317, pl. 4, figs. 25, 26, 29.

? *Rectobolivina bifrons* (Brady). Matsunaga, 1963, pl. 41, figs. 8a, b; Saidova, 1975, pl. 86, figs. 9, 10.

not *Rectobolivina bifrons* (Brady). LeRoy, 1964, p. F34, pl. 3, figs. 1, 2; Loeblich and Tappan, 1964, p. C553, fig. 438, nos. 2a-5b.

not *Rectobolivina* cf. *bifrons* (Brady). McCulloch, 1977, p. 259, pl. 107, figs. 17a, b.

**Material.**—IGUT14492, sample MK19 (Figure 4.3a-c); IGUT14493, sample MK19 (Figure 4.4a-c); IGUT14494, sample MK19 (Figure 8.2); IGUT14495, sample MK19





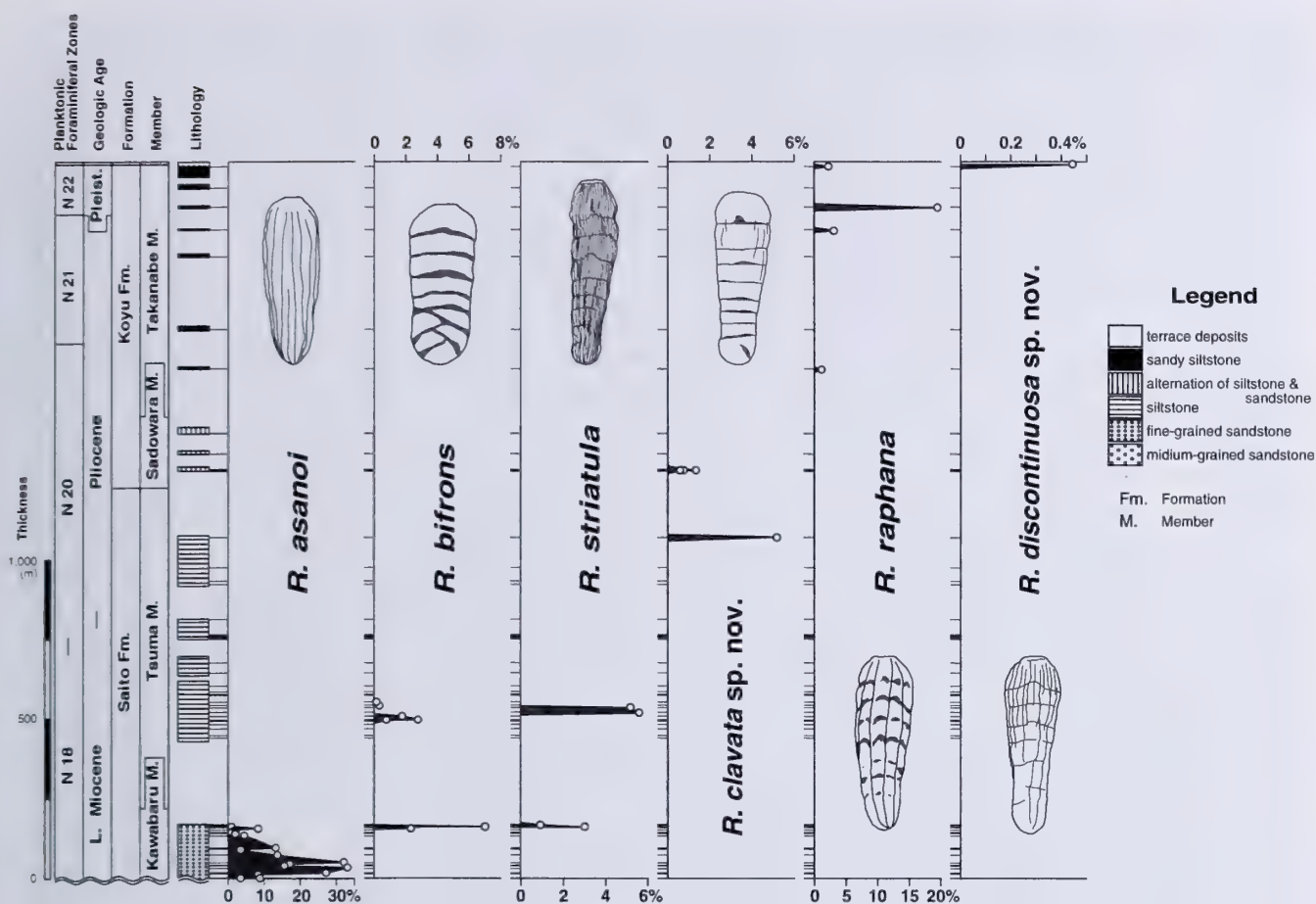
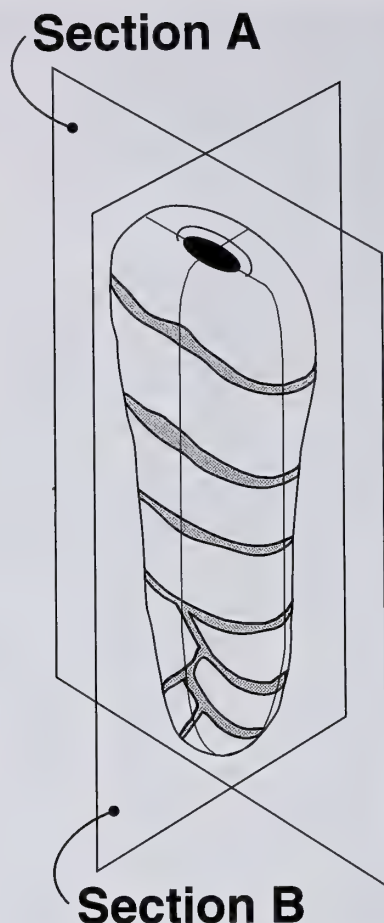


Figure 5. Stratigraphic occurrence and percentage abundance of six *Rectobolivina* species in the study section of the Miyazaki Group.

Figure 4. 1a-c. Megalospheric form of *Rectobolivina asanoi* (Murata), IGUT14488. 1a: side, 1b: apertural views,  $\times 60$ . 1c: Optical microphotograph of 1a,  $\times 60$ . 2a-c. Microspheric form of *Rectobolivina asanoi* (Murata), IGUT14489. 2a: side, 2b: apertural views,  $\times 60$ . 2c: Optical microphotograph of 2a,  $\times 60$ . 3a-c. Megalospheric form of *Rectobolivina bifrons* (Brady), IGUT14492. 3a: side, 3b: apertural views,  $\times 60$ . 3c: Optical microphotograph of 3a,  $\times 60$ . 4a-c. Microspheric form of *Rectobolivina bifrons* (Brady), IGUT14493. 4a: side, 4b: apertural views,  $\times 60$ . 4c: Optical microphotograph of 4a,  $\times 60$ . 5a-c (holotype), IGUT14499, and 6a-c (paratype), IGUT14500. Megalospheric form of *Rectobolivina clavata* sp. nov., 5a: side, 5b: apertural views,  $\times 60$ . 5c: Optical microphotograph of 5a,  $\times 60$ ; 6a: side, 6b: apertural views,  $\times 50$ . 6c: Optical microphotograph of 6a,  $\times 50$ . 7a-c. Microspheric form of *Rectobolivina clavata* 2p. nov., IGUT14501. 7a: side, 7b: apertural views,  $\times 50$ . 7c: Optical microphotograph of 7a,  $\times 50$ . 8a-c. Megalospheric form of *Rectobolivina discontinuosa* sp. nov. (holotype), IGUT14504. 8a: side, 8b: apertural views,  $\times 50$ . 8c: Optical microphotograph of 8a,  $\times 50$ . 9a-c. Microspheric form of *Rectobolivina discontinuosa* sp. nov. (paratype), IGUT14505. 9a: side, 9b: apertural views,  $\times 50$ . 9c: Optical microphotograph of 9a,  $\times 50$ . 10a-c and 11a-c. Megalospheric form of *Rectobolivina raphana* (Parker and Jones), IGUT14508 and IGUT14509. 10a: side, 10b: apertural views,  $\times 50$ . 10c: Optical microphotograph of 10a,  $\times 50$ ; 11a, IGUT14509: side, 11b: apertural views,  $\times 50$ . 11c: Optical microphotograph of 11a,  $\times 50$ . 12a-c. Megalospheric form of *Rectobolivina striatula* (Cushman), IGUT14513. 12a: side, 12b: apertural views,  $\times 50$ . 12c: Optical microphotograph of 12a,  $\times 50$ .



**Figure 6.** Diagram showing the two sections of a foraminiferal test used in this study.

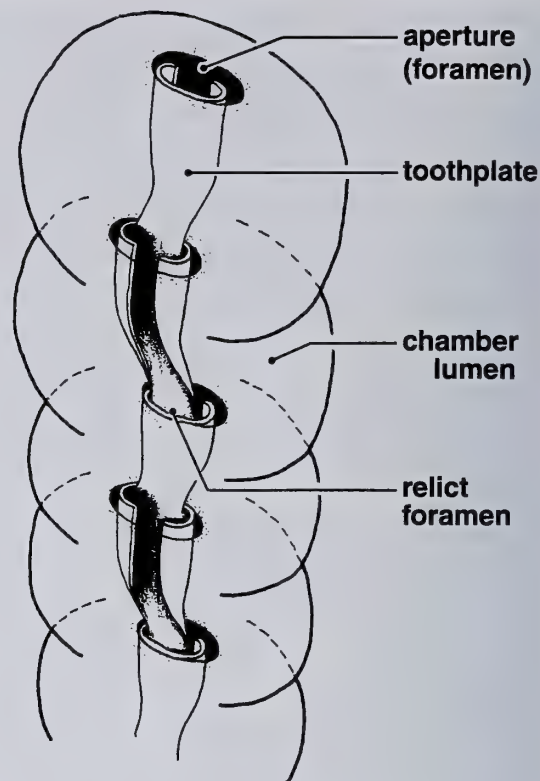
(Figure 8.3); IGUT14496, sample MK19 (Figure 8.4); IGUT14497, sample MK19 (Figures 8.5, 9.1–9.2); IGUT 14498, sample MK19 (Figures 9.4–9.5).

**Remarks.**—This species was first described by Brady (1881) from off the Pacific coast of central Japan, and the original figures by Brady (1884) are reproduced in Figure 13.2–13.4b. Cushman (1913) examined both megalospheric and microspheric forms of the species and pointed out that all Brady's original figures represent megalospheric forms. Many specimens treated here are megalospheric forms (e.g. Figure 4.3a–c), which compare well with Brady's original figures. The megalospheric form is much shorter than the microspheric one, because of the reduced chamber number at the biserial stage.

***Rectobolivina clavata* sp. nov.**

Figures 4.5a–c, 4.6a–c, 4.7a–c; 10.3, 10.4

? *Rectobolivina bifrons* (Brady). LeRoy, 1964 (non *Sagrina*



**Figure 7.** A schematic sketch of the *Rectobolivina* species showing the relationship among toothplate, foramina and chamber lumina in the uniserial stage. Terms follow Revets (1989, 1993).

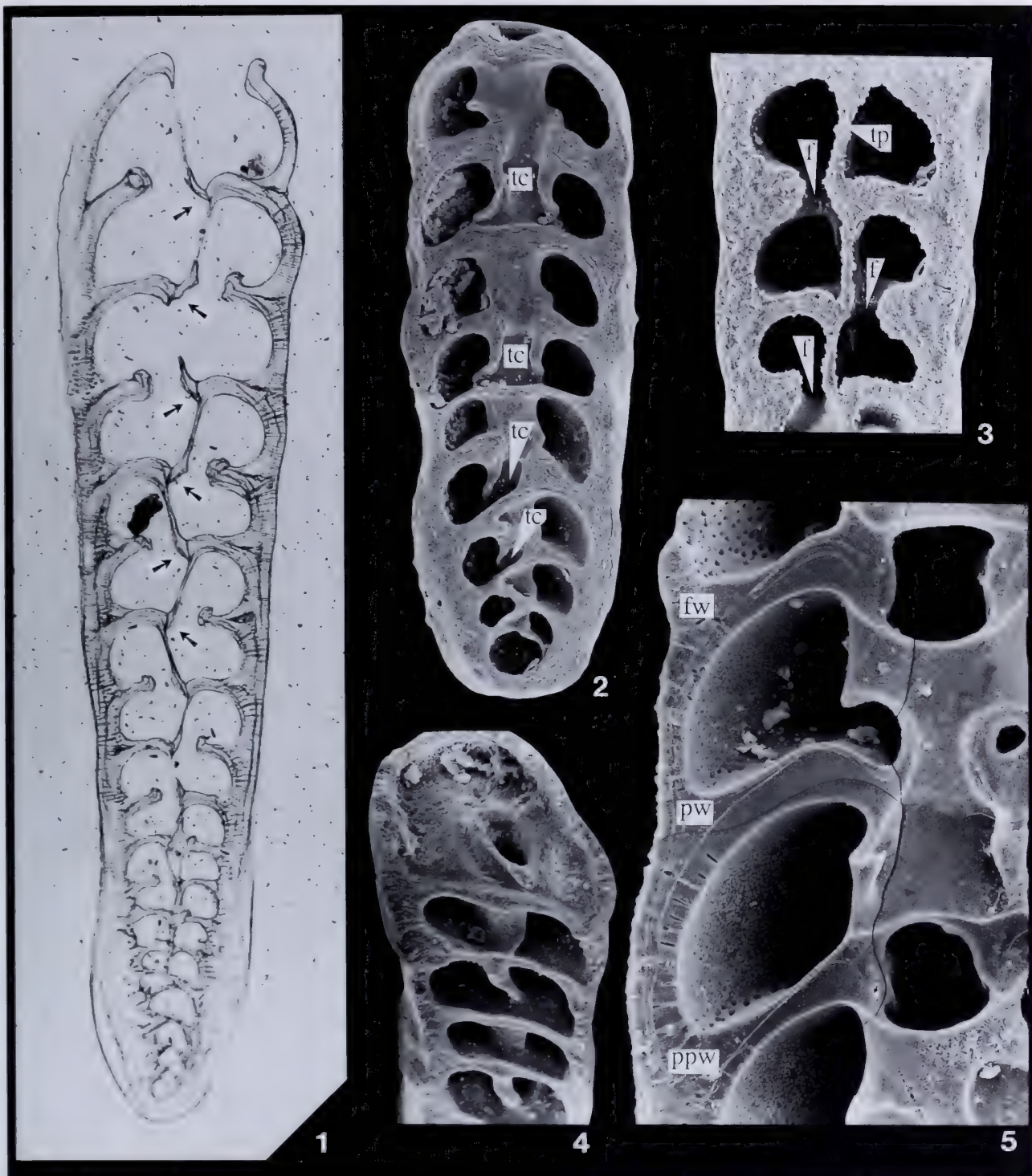
*bifrons* Brady, 1881), p. F34, pl. 3, figs. 1, 2.

**Diagnosis.**—A species of *Rectobolivina* with a clavate-shaped and inornate test.

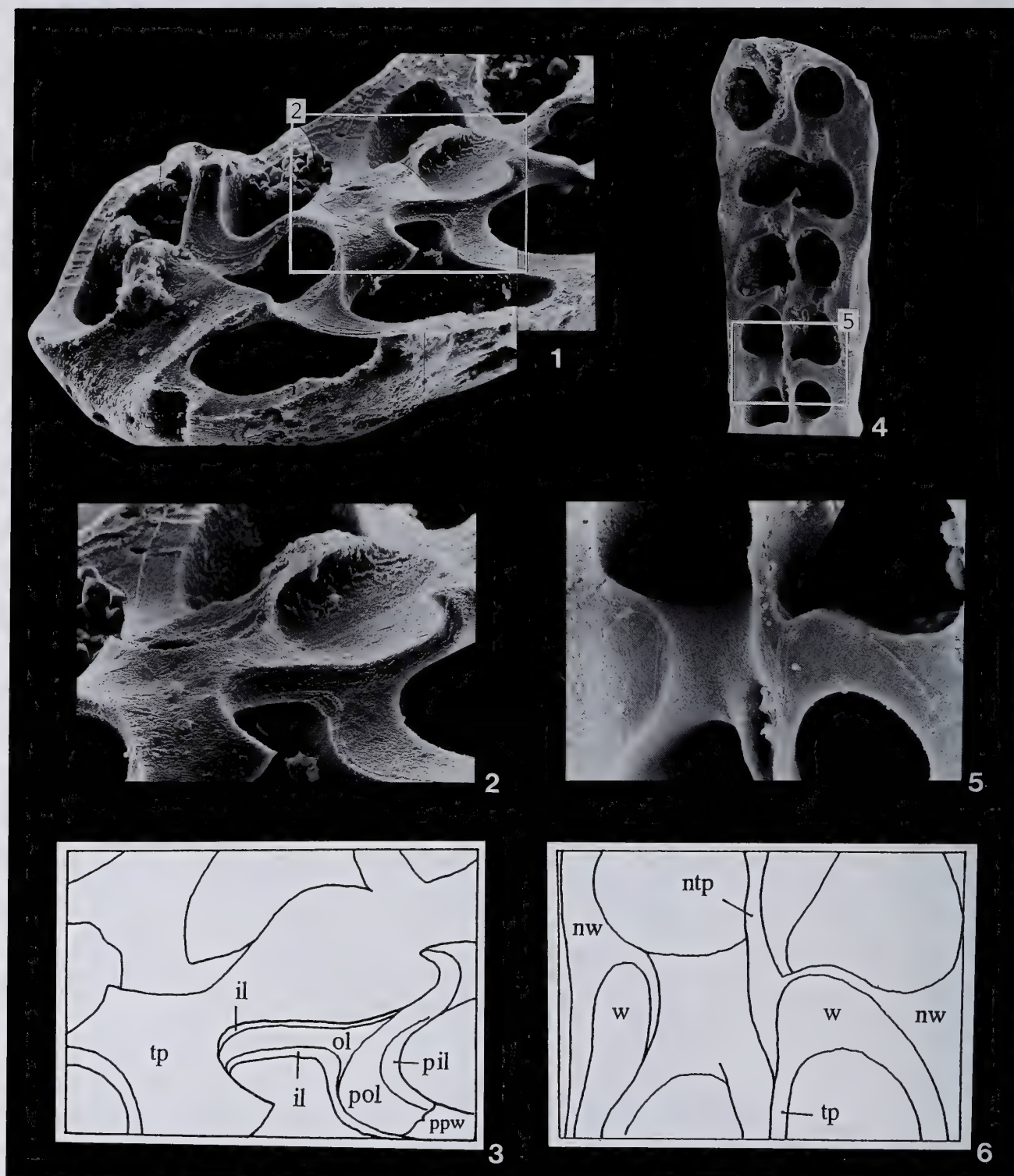
**Description.**—Test free, moderate size, approximately four times as long as broad, straight, clavate in shape, elliptical in being laterally depressed in cross section, initial end bluntly rounded in megalospheric form, whereas initial end pointed in microspheric form; chambers numerous, breadth twice the height, gradually increasing in size added changing from uniserial to biserial, after the third chamber in megalospheric form or after the tenth chamber in microspheric form; wall calcareous, optically radial, transparent or semitransparent, finely perforate, rather thick, sometimes very weakly striate in later part of test; sutures distinct, moderately thick, slightly depressed; aperture terminal, nearly circular to elliptical opening, with a distinct but slightly protruding lip; intercameral septa thick as well as the wall, parallel to slightly arched; toothplate folded at the lateral edge, extending into the preceding aperture (foramen), its folded face arranged alternately in planes 180° apart.

**Material.**—Holotype: IGUT14499 (1.03 mm in length,



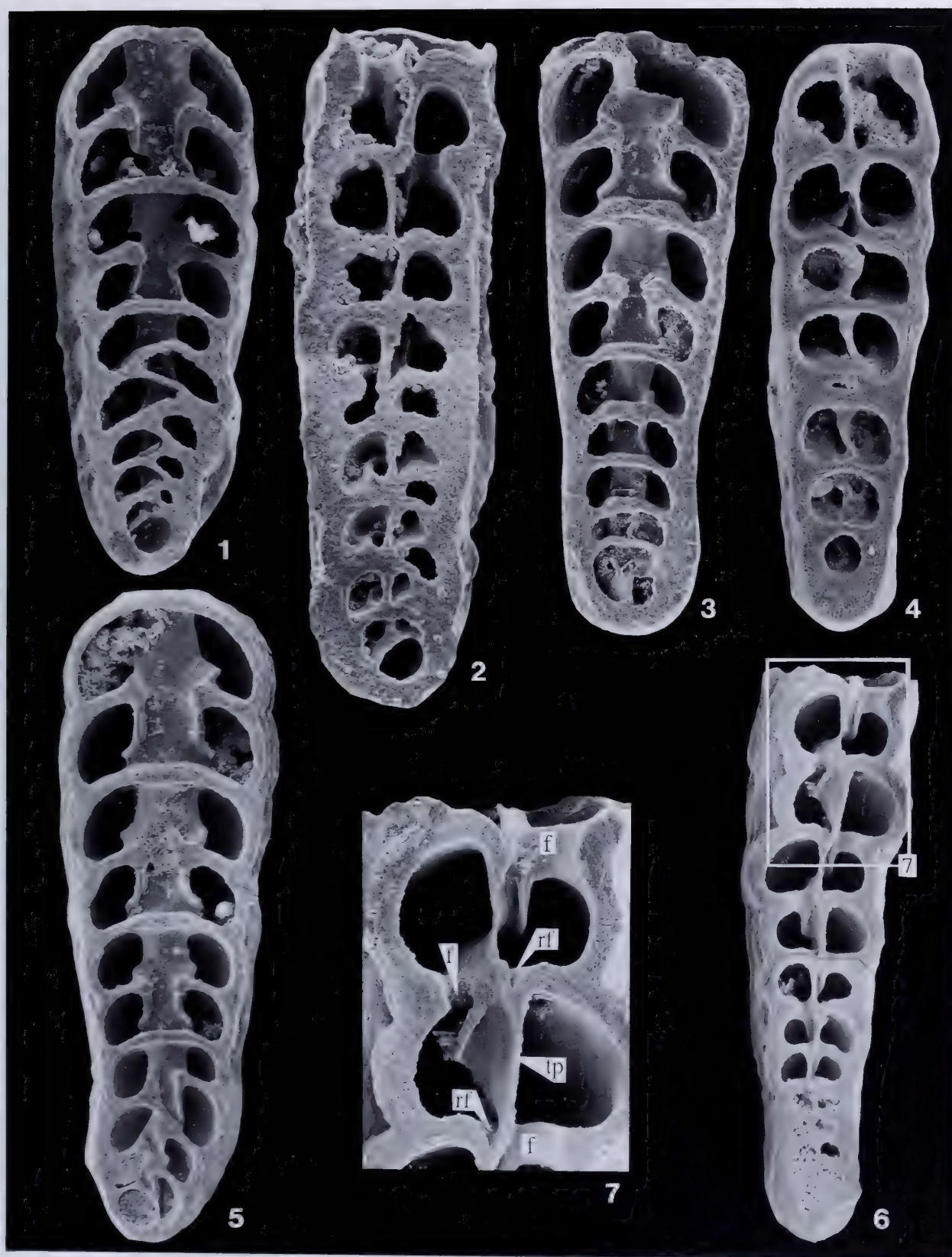


**Figure 8.** Sections of the microspheric form of *Rectobolivina raphana* (Parker and Jones) (8.1) and the megalospheric forms of *Rectobolivina bifrons* (Brady) (8.2–8.5), IGUT14494–IGUT14497. **1.** Overall view of Section B (Figure 6). Arrows indicate the attached portion of the toothplates, which never continuously extend from the preceding toothplate or septa,  $\times 143$ . **2.** Overall view of Section A. Concave side of trough-shaped plate (tc) which rotates  $180^\circ$  between chambers,  $\times 180$ . **3.** A part of the uniserial stage in Section B. Foramen (f) opens alternately along toothplate (tp). Toothplate always runs along the centre of chamber lumen,  $\times 350$ . **4.** Oblique section showing relationship between foramen and toothplate,  $\times 250$ . **5.** A part of test wall showing lamellar development of test wall according to test growth. Final chamber wall (fw) covers wall of penultimate chamber (pw), and pw covers over the pre-penultimate chamber wall (ppw),  $\times 500$ .



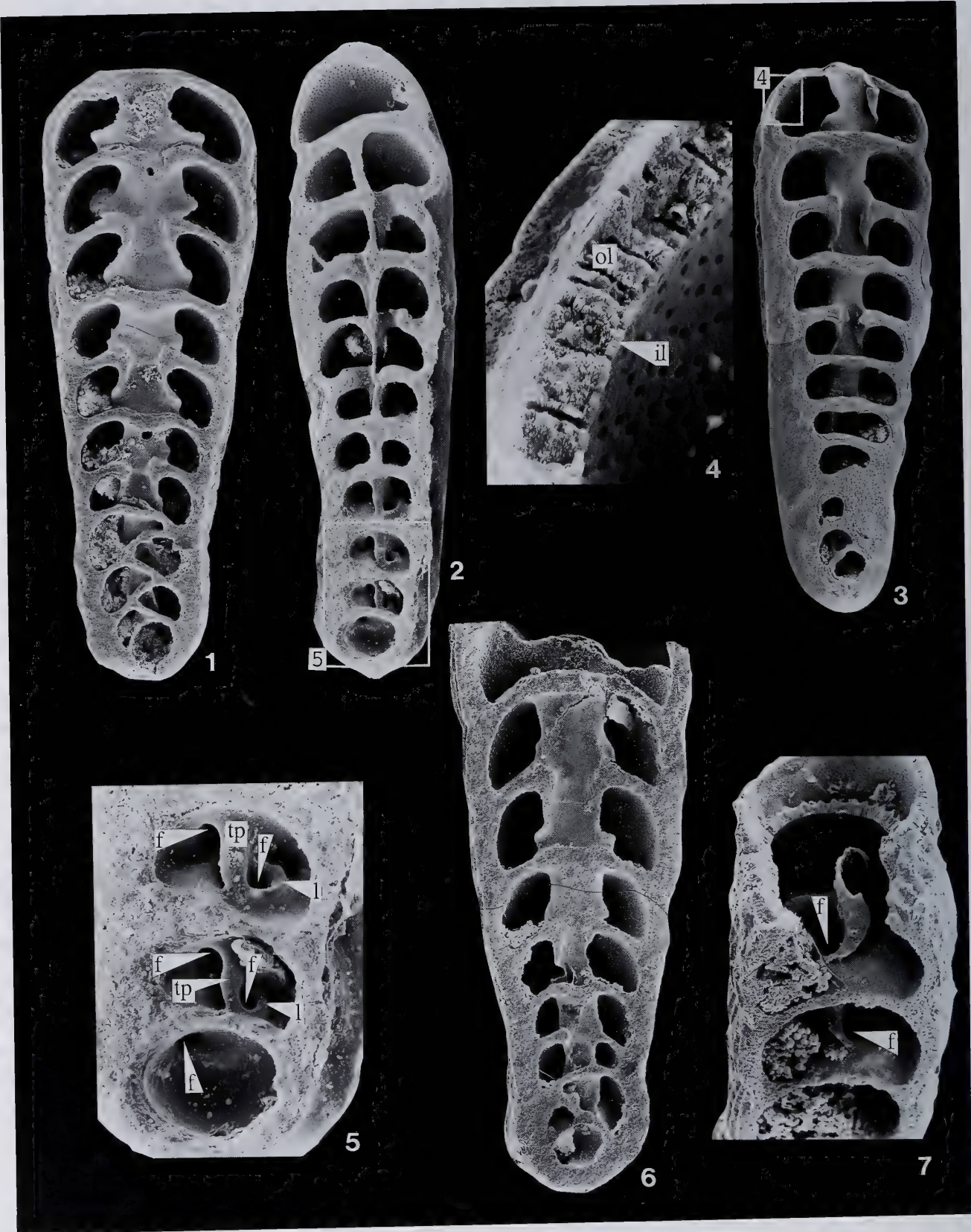
**Figure 9.** Megalospheric forms of *Rectobolivina bifrons* (Brady). 9.1, 9.2, IGUT14497. **1.** Oblique view of later part of test of the same specimen shown in Figure 8.5,  $\times 450$ . **2, 3.** Close-up photograph and its sketch, showing lamellar structure of toothplate (tp) in the penultimate chamber. A thick outer lamella (ol) is intercalated with two inner lamellae (il), and attaches to pre-penultimate chamber wall (ppw) composed of previous outer (pol) and inner layers (pil),  $\times 800$ . **4, 5.** IGUT14498, 4. A part of the uniserial stage in Section B (Figure 6),  $\times 180$ . **5, 6.** Close-up photograph and its sketch, are showing the attachment portion of toothplate (tp). Toothplate (tp), a part of chamber wall (w), is separated from next toothplate (ntp) which is a part of next chamber wall (nw),  $\times 700$ .



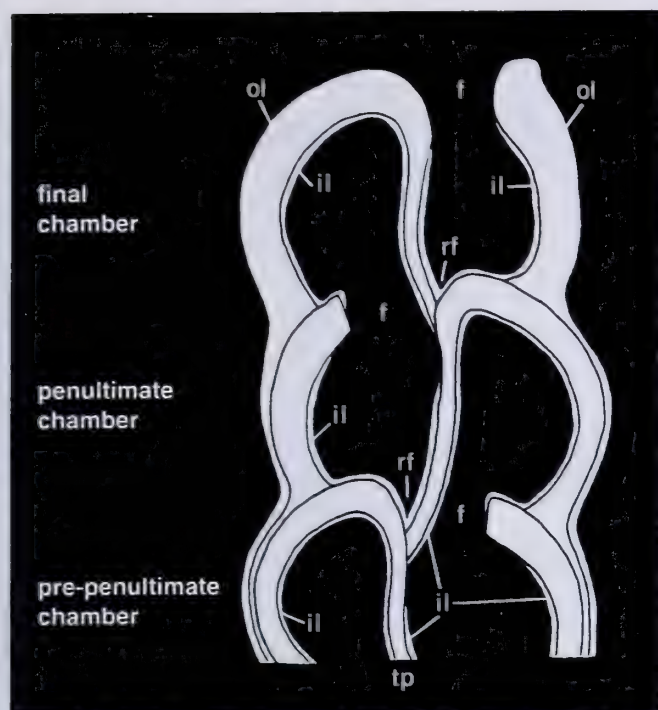


**Figure 10.** All dissected specimens are the megalospheric forms. 1, 2. Sections A and B (see Figure 6) of *Rectobolivina asanoi* (Murata), respectively, IGUT14490 and IGUT14491,  $\times 150$  and  $200$ . 3, 4. Sections A and B of *Rectobolivina clavata* sp. nov., respectively, IGUT14502 and IGUT14503,  $\times 150$  and  $200$ . 5, 6. Sections A and B of *Rectobolivina discontinuosa* sp. nov., respectively, IGUT14506 and IGUT14507,  $\times 120$ . 7. Close-up of a part of 6, showing the relationship among toothplate (tp), foramen (f) and relict foramen (rf),  $\times 250$ .









**Figure 12.** A schematic figure of the lamellar structure of the test wall and the toothplate in Section B (see Figure 6), showing foramen (f), toothplate (tp), outer lamella (ol), inner lamella (il), and relict foramen (rf). The terms used in the figure mostly follow Revets (1989, 1993).

0.36 mm in maximum breadth), sample MK48 (Figure 4.5a-c). Paratypes: IGUT14500 (0.92 mm in length, 0.32 mm in maximum breadth), sample MK48 (Figure 4.6a-c); IGUT14501 (1.08 mm in length, 0.34 mm in maximum breadth), sample MK48 (Figure 4.7a-c); IGUT14502, sample MK48 (Figure 10.3); IGUT14503, sample MK48 (Figure 10.4).

**Etymology.**—The specific name, *clavata*, is derived from the clavate-shape of the test.

**Remarks.**—This new species has a more slender and more clavate-shaped test than *R. bifrons* (Brady). According to measurements of the test width (TW) in megalospheric forms of *R. bifrons* and *R. clavata* (Figure 14), the test width of *R. clavata* becomes narrowest at the fourth chamber, whereas that of *R. bifrons* constantly increases (Figure 15). Furthermore, the former has a single pair of biserial chambers, whereas the latter has several

pairs of biserial chambers. *R. clavata* differs from *Rectobolivina columellaris* (Brady, 1881) in having a more compressed test, in contrast to the cylindrical test of the latter species. An Australian *Rectobolivina* species, described as *Sagrina sydneyensis* by Goddard and Jensen (1907), differs from *R. clavata* in having ornamentation with minute spines and some large pores.

### *Rectobolivina striatula* (Cushman, 1913)

Figures 4.12a-c; 11.6, 11.7; 13.11a, b

*Siphogenerina striatula* Cushman, 1913, p. 108, pl. 47, fig. 1.

*Rectobolivina bifrons* (Brady) var. *striatula* (Cushman, 1917).

LeRoy, 1964 (non *Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917, nomen nudum), p. F34, pl. 3, figs. 5, 6.

? *Rectobolivina bifrons* (Brady) var. *striatula* (Cushman, 1917).

LeRoy, 1941a (non *Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917, nomen nudum), p. 35, pl. 2, figs. 7, 8.

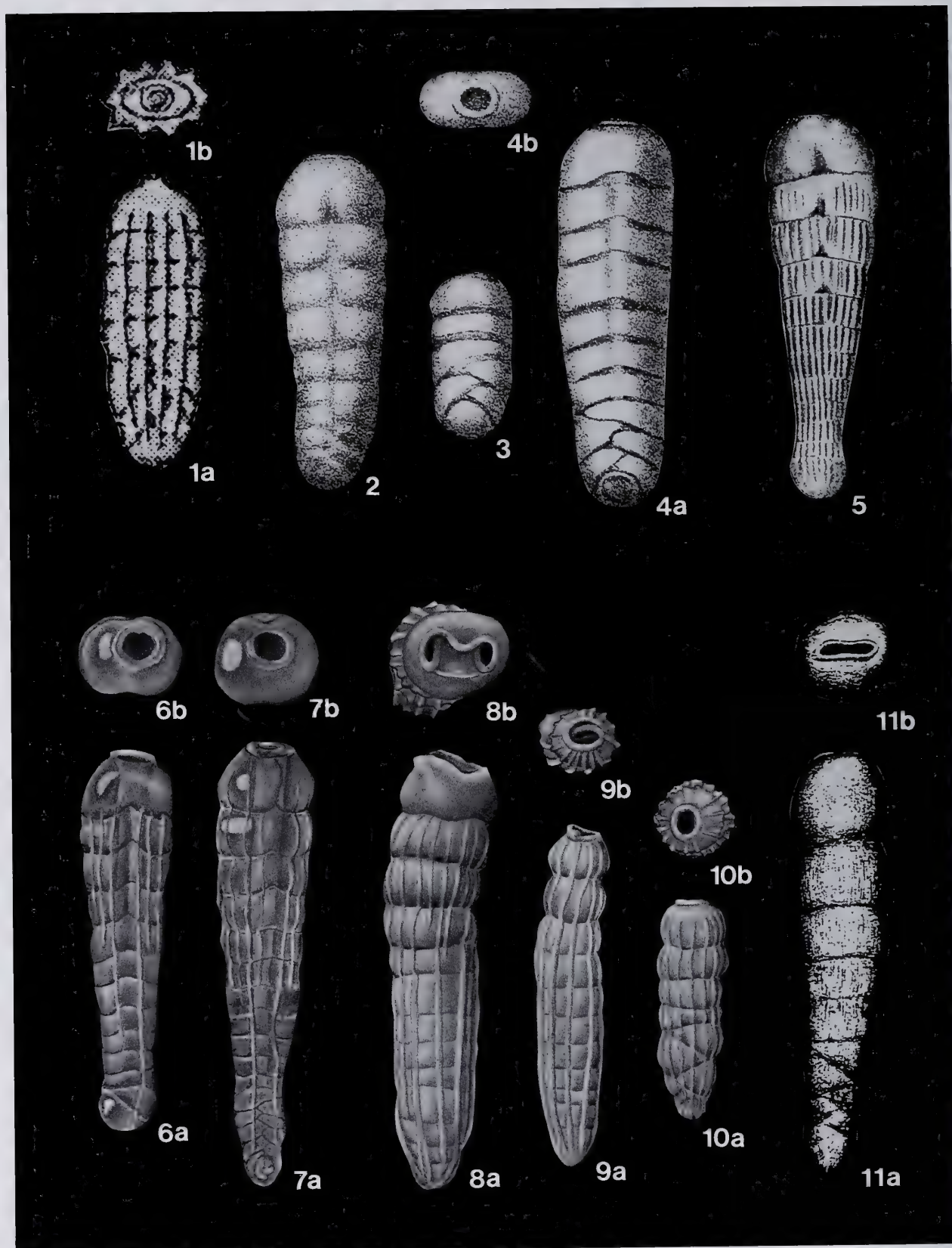
not *Rectobolivina striatula* (Cushman, 1917) (non *Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917, nomen nudum). Carter, 1964, p. 69, pl. 2, figs. 35, 36; Hornibrook, 1968, p. 73, fig. 13 (part), Hayward and Buzas, 1979, p. 72, pl. 26, figs. 320, 321.

not *Rectobolivina striatula* (Cushman, 1913). Kennett, 1966 (non *Siphogenerina striatula* Cushman, 1913), p. 47, fig. 59.

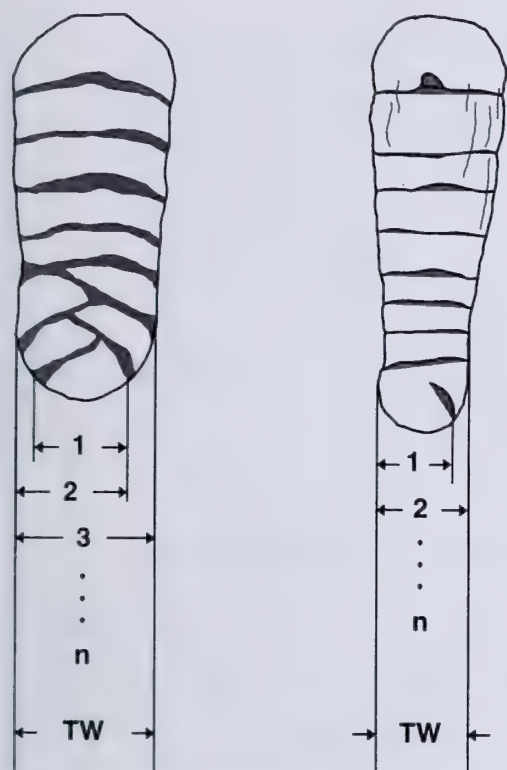
**Material.**—IGUT14513, sample MK19 (Figure 4.12a-c); IGUT14514, sample MK19 (Figure 11.6); IGUT14515, sample MK19 (Figure 11.7).

**Remarks.**—All specimens of the present species from the Miyazaki Group are regarded as megalospheric forms because they are characterized in having a bluntly rounded initial end (Figure 4.12a, c) and three pairs of biserial chambers at the earliest part (Figure 11.6). This species is distinguished from the other *Rectobolivina* species in having numerous, fine, and longitudinal striations covering the test surface (Figure 4.12a). Compared with Cushman's (1913) original figure of the type specimen (here reproduced in Figure 13.11a, b), our specimens have a slightly rhomboidal outline in section and an elliptically rounded aperture, in contrast to the rounded outline and rather narrow slit-like aperture in the type specimen.

◀ **Figure 11.** All dissected specimens are megalospheric forms. 1, 2. Sections A and B (see Figure 6) of *Rectobolivina raphana*, respectively, IGUT14510 and IGUT14511.  $\times 120$  and 150. 3. Section A of *R. raphana*, IGUT14512,  $\times 120$ . 4. Close-up of final chamber wall of figure 3,  $\times 1,500$ . ol: outer layer, il: inner layer. 5. Close-up view of the biserial part in *R. raphana*,  $\times 400$ . f: foramen, tp: toothplate, l: lip. 6. Section A of *Rectobolivina striatula* (Cushman), IGUT14514,  $\times 180$ . 7. Oblique view of foramen and toothplate in *R. striatula*, IGUT14515. The toothplate extends into the chamber lumen. Its lateral edges strongly fold towards the opposite side of the preceding foramen opening (f), but it never shows the tube-like structure.  $\times 180$ .





***R. bifrons******R. clavata* sp. nov.**

**Figure 14.** Definition of measurements. TW: Test width including the distal chambers, n: Number of chambers from the initial to final chamber.

***Rectobolivina clavatriatula* nom. nov.**

Figure 13.5

*Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917, p. 662 (nomen nudum); Cushman, 1919, p. 620; Cushman, 1921, p. 278, pl. 56, fig. 4; Cushman, 1926, p. 18, pl. 2, fig. 6, pl. 4, figs. 1–3.

*Rectobolivina bifrons* (Brady) var. *striatula* (Cushman, 1917). Cushman, 1937, p. 205, pl. 23, figs. 17, 18.

**Diagnosis.**—A species of *Rectobolivina* with a clavate-shaped test covered by distinct longitudinal striations.

**Etymology.**—The new specific name, *clavatriatula*, represents clavate test shape and distinct striations of this species.

**Remarks.**—Cushman (1917) reported this species from the Sogod Bay (~1,000 m water depth), Philippines, under the name of *Siphogenerina bifrons* (Brady) var. *striatula* Cushman. Later, Cushman (1921, pl. 56, fig. 4) illustrated it (here reproduced in Figure 13.5). However, *S. bifrons* var. *striatula* Cushman, 1917 is a junior primary homonym of *Siphogenerina striatula* Cushman, 1913 (the original figure of the holotype is reproduced in Figure 13.11a, b), reported from the western Pacific Ocean. The former can clearly be distinguished from the latter in having a clavate-shaped test with fewer but more raised striations on the test surface. Consequently, *Rectobolivina clavatriatula* is proposed as a new name to replace *S. bifrons* var. *striatula* Cushman, 1917.

***Rectobolivina discontinuosa* sp. nov.**

Figures 4.8a–c, 9a–c; 10.5–10.7; 13.6a, 13.7b

*Rectobolivina bifrons* (Brady) (non *Sagrina bifrons* Brady, 1881).

Loeblich and Tappan, 1964, p. C553, fig. 438, nos. 2a–5b;

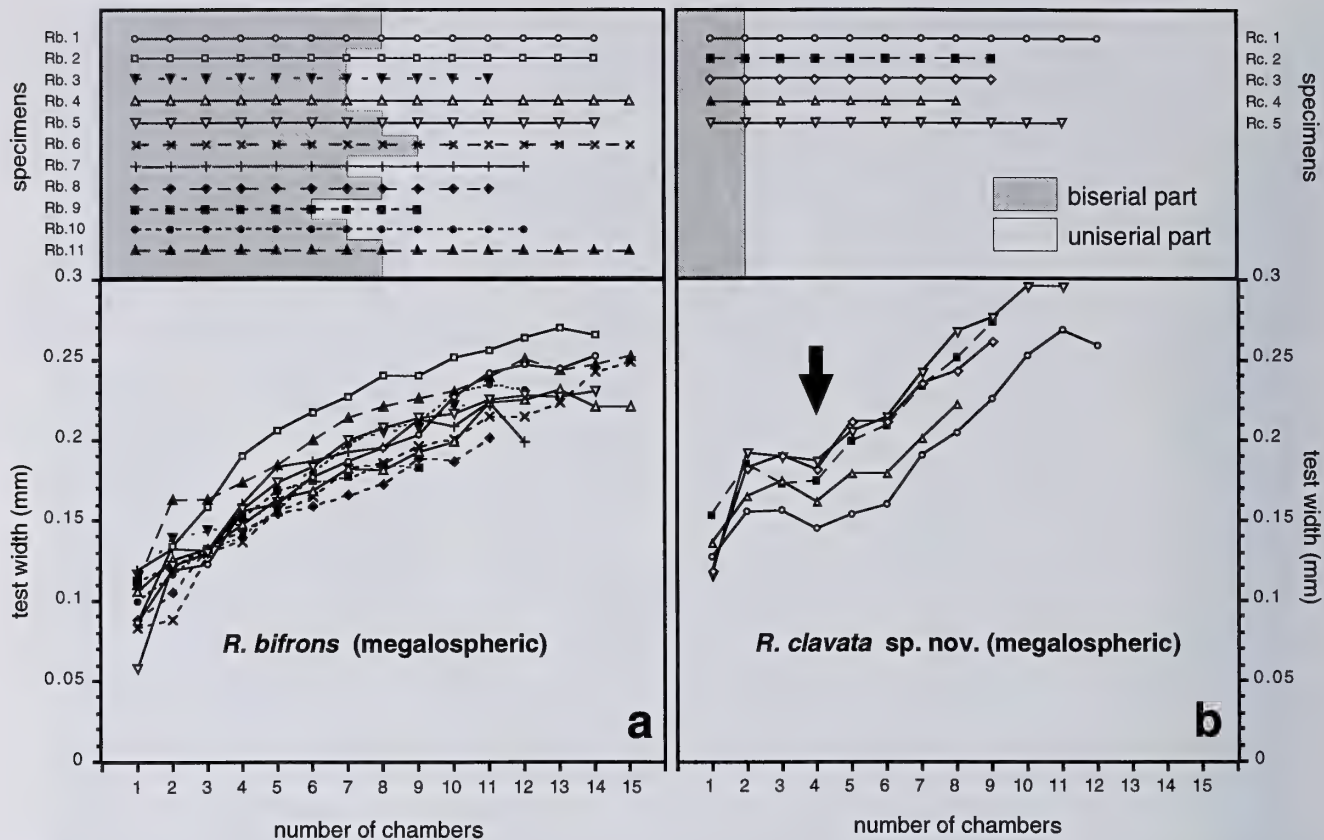
Loeblich and Tappan, 1987, p. 517, pl. 567, figs. 11–14 (not figs. 15–17).

? *Rectobolivina bifrons* (Brady) var. *striatula* (Cushman). LeRoy, 1941b (non *Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917, nomen nudum), p. 80, pl. 1, fig. 9.

**Diagnosis.**—A species with a clavate-shaped test, whose surface is covered by numerous and discontinuous striations mainly on the later portion of the test.

**Description.**—Test free, moderate size, approximately four times as long as broad, straight, clavate-shaped, elliptical in being laterally depressed in cross section, initial end bluntly rounded in megalospheric form, pointed in microspheric form; chambers numerous, breadth twice the height, gradually increasing in size, changing from biserial to uniserial after the seventh chamber in megalospheric forms or after the thirteenth chamber in microspheric forms; wall calcareous, optically radial, transparent or semitransparent, finely perforate, rather thick, striae numerous in the later part of the test but much sparser in the earlier part of the test; sutures distinct, moderately thick, slightly depressed or flush; aperture terminal, nearly circular to elliptical, with a distinct lip; intercameral septa thick as well as the wall, parallel to slightly arched; toothplate folded at the side edge, extending into the preceding aperture (foramen), its folded face arranged alternately in position in planes 180° apart.

← **Figure 13.** Reproduction of original figures of the studied species. **1a, b.** *Rectobolivina asanoi* Murata, 1951,  $\times 135$ . **2 4b.** *Rectobolivina bifrons* (Brady, 1881), after Brady (1884),  $\times 71$ . **5.** *Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917, after Cushman (1921) = *Rectobolivina clavatriatula* nom. nov.,  $\times 66$ . **6a–7b.** *Rectobolivina bifrons* (Brady, 1881) of Loeblich and Tappan (1964) = *Rectobolivina discontinuosa* sp. nov.,  $\times 66$ . **6a, b:** megalospheric, **7a, b:** microspheric forms. **8a–10b.** *Rectobolivina raphana* (Parker and Jones, 1865) of Loeblich and Tappan (1964),  $\times 55$ . **11a, b.** *Siphogenerina striatula* Cushman, 1913,  $\times 75$ .



**Figure 15.** Test width changes in the megalospheric forms of *Rectobolivina clavata* sp. nov. ( $n = 5$ ) and *R. bifrons* ( $n = 11$ ) through ontogeny. Arrow indicates the position where the test width of *R. clavata* becomes the narrowest.

**Material.**—Holotype: IGUT14504 (0.98 mm in length, 0.31 mm in maximum breadth), sample MK57 (Figure 4.8a–c). Paratypes: IGUT14505 (1.05 mm in length, 0.31 mm in maximum breadth), sample MK57 (Figure 4.9a–c); IGUT14506, sample MK57 (Figure 10.5); IGUT14507, sample MK57 (Figure 10.6, 10.7).

**Etymology.**—The new specific name, *discontinua*, comes from the discontinuous striations of the test.

**Remarks.**—The specimens treated here (Figures 4.8a–c, 9a–c) are compared well with those of Loeblich and Tappan's (1964, 1987) *Rectobolivina bifrons* (here reproduced in Figures 13.6a–7b) in having a clavate-shaped test ornamented by distinct, discontinuous striations. This discontinuous striation is clearly distinguished from the completely continuous striation in typical *Rectobolivina clavatostriatula* (Figure 13.5) and from the inornate test of *Rectobolivina clavata* (Figure 4.5a–c, 4.6a–c, 4.7a–c). Therefore, we judge our specimens to belong to a new species and not to either of the latter two species. This new species differs from *Rectobolivina asanoi* Murata, 1951 by its more slender and clavate-shaped test with less raised striations on the test surface.

### *Rectobolivina raphana* (Parker and Jones, 1865)

Figures 4.10a–c, 4.11a–c; 8.1; 11.1–11.5; 13.8a–13.10b

*Uvigerina* (*Sagrina*) *raphanus* Parker and Jones, 1865, p. 364, pl. 18, figs. 16, 17.

*Sagrina raphanus* (Parker and Jones). Brady, 1884, p. 585, pl. 75, figs. 21–24.

*Siphogenerina* (*Sagrina*) *raphanus* (Parker and Jones). Cushman, 1913, p. 108, pl. 46, figs. 1–5.

*Siphogenerina raphanus* (Parker and Jones). Cushman, 1921, p. 280, pl. 56, fig. 7; Cushman, 1926, p. 4, pl. 1, figs. 3, 4 (? figs. 1, 2), pl. 2, figs. 1–3, 10, pl. 5, figs. 1, 2; Cushman, 1942, p. 55, pl. 15, figs. 8, 9 (not figs. 6, 7); Hofker, 1951a, p. 233, figs. 155, 156; LeRoy, 1964, p. F35, pl. 3, fig. 35.

*Siphogenerina raphana* (Parker and Jones). Hada, 1931, p. 134, text-figs. 91a, b; Asano, 1950, p. 14, figs. 56, 57; Asano, 1958, p. 30, pl. 7, figs. 8–10; Kuwano, 1962, pl. 22, fig. 5; Ishiwada, 1964, pl. 5, fig. 81.

*Rectobolivina raphana* (Parker and Jones). Loeblich and Tappan, 1964, p. 533, fig. 438–9–11; Matoba, 1970, p. 60, pl. 3, fig. 31; Whittaker and Hodgkinson, 1979, p. 56, fig. 8; Matoba and Honma, 1986, pl. 4, figs. 6a, b; Matoba and Fukusawa,



1992, p. 218, fig. 9-6.

? *Siphogenerina* (*Sagrina*) *raphanus* (Parker and Jones). Egger, 1893, p. 317, pl. 9, fig. 36.

**Material.**—IGUT14508, sample MK56 (Figure 4.10a-c); IGUT14509, sample MK56 (Figure 4.11a-c); sample MK56 (Figure 8.1); IGUT14510, sample MK56 (Figure 11.1); IGUT14511, sample MK56 (Figure 11.2, 11.5); IGUT14512, sample MK56 (Figure 11.3, 11.4).

**Remarks.**—All specimens treated in this study are elliptically rounded in section, and in this respect, they are distinguished from the paratypes of this species designated by Loeblich and Tappan (1964) (here reproduced in Figure 13.8a-13.10b). Unfortunately, they did not show a figure of the lectotype. As was shown in many previous descriptions (see the above synonym list), strongly raised costae on the entire test surface are recognized in all specimens examined (e.g. Figure 4.10a-4.11c).

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## 行 事 予 定

㊟第152回例会は、2003年1月24日（金）～26日（日）に横浜国立大学教育人間科学部にて開催の予定です。1月24日（金）にシンポジウムとして「白亜紀海洋無酸素事件の解明：世話人 平野弘道・北里 洋・西 弘嗣」が、また1月25日（土）にシンポジウム「中・古生代微化石研究の現状と将来－テレーン解析後の使命－：世話人 指田勝男」が開催されます。なお、講演の申し込み締め切りは、2002年11月29日（金）です。講演申し込みの予稿集原稿送付の際には発表で使用する機器（液晶プロジェクター、OHP、スライドなど）の希望について明記して下さい。

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### CONTENTS

- Takashi Matsubara:** Molluscan fauna of the "Miocene" Maéjima Formation in Maéjima Island, Okayama Prefecture, southwest Japan ..... 127
- Satoshi Hanagata:** Eocene shallow marine foraminifera from subsurface sections in the Yufutsu-Umaoi district, Hokkaido, Japan ..... 147
- Toshiyuki Kimura:** Feeding strategy of an Early Miocene cetothere from the Toyama and Akeyo Formations, central Japan ..... 179
- Subhash Chandar Khosla and Madan Lal Nagori:** Ostracodes from the Inter-trappean beds (Early Paleocene) of the east coast of India ..... 191
- Hisayoshi Kato:** Fossil crabs (Crustacea: Decapoda: Brachyura) from the latest Miocene Senhata Formation, Boso Peninsula, Japan ..... 211
- Shungo Kawagata and Akio Hatta:** Internal test morphology of the genus *Rectobolivina* (Cushman, 1927) from the Late Cenozoic Miyazaki Group, southwestern Japan ..... 219



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Cover: Typical Pleistocene fossils from the Japanese Islands. Front cover: *Sinomegaceros yabei* (Shikama). Back cover: *Paliurus nipponicum* Miki, *Mizuhopecten tokyoensis* (Tokunaga), *Neodenticula seminae* (Simonsen and Kanaya) Akiba and Yanagisawa and *Emiliana huxleyi* (Lohmann) Hay and Mohler.

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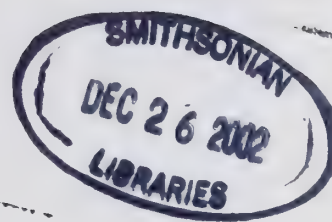


# Enamel microstructure of some fossil and extant murid rodents of India

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**Abstract.** Spatial arrangement of various enamel types (*schmelzmuster*) present in the incisors and molars of some fossil and extant murid rodents of India was studied from both the functional and phylogenetic points of view. Hunter-schreger bands (HSBs) along with radial enamel (RE) in mice molars have been found to occupy the entire height of the enamel crown (from the base to the top) on the anterior and the posterior portions. These HSBs tend to be horizontal around the base and inclined apically around the top. A clear distinction between the leading and the trailing edges of chewing surfaces based on the difference in the orientation of prisms has been observed in hypsodont murid molars. On the leading edges, the long axes of prisms originating from the enamel-dentine junction tend to be oriented towards the load, whereas those on the trailing edges turn away from the load. The *schmelzmuster* in molars of *Mus*, indicate an omnivorous diet, whereas that in *Golunda*, *Millardia*, and *Bandicota* points to adaptation for an abrasive diet. The Indian bandicoot rat (*Bandicota*) with its large, hypsodont molars has developed horizontally oriented (relative to the occlusal surface) HSBs at the base of the enamel crown. These HSBs have been found in enamel layers oriented both almost parallel and perpendicular to the occlusal surface, an observation that corroborates the presence of horizontal tension at the base of the tooth due to vertical load on the occlusal surface. In the light of the observations made here, a model depicting changes in *schmelzmuster* in murid rodents through Late Miocene and Plio-Pleistocene times is suggested.

**Key words:** enamel microstructure, functional morphology, India, Muridae, phylogeny, rodent

## Introduction

The enamel microstructure can be studied at various hierarchical levels (Koenigswald and Clemens, 1992; Carlson, 1990). Dental enamel in all mammals is made up of hydroxyapatite 'crystallites'. These fiber-like crystallites are arranged almost parallel to each other to form bundles called 'prisms' and these in turn are surrounded by an 'interprismatic matrix' (IPM) which is also made up of crystallites (Wahlert and Koenigswald, 1985). The crystallites of IPM may or may not run parallel to the prism they surround (Martin, 1990). Because of the difference in the orientation of prism and interprismatic crystallites, distinct prism boundaries called as 'prism sheathes' are formed. The path of a prism can be traced from the enamel-dentine junction (EDJ), through the entire thickness of the enamel, terminating at the outer surface. 'Enamel types' are defined by the spatial arrangement of groups of prisms. The part of the enamel in which prisms run parallel to each other is termed 'radial enamel' (RE) (Koenigswald, 1977). In many mammals, prisms are

arranged in layers or zones, and when prisms of alternate layers run in different directions, a decussating structure is produced called 'Hunter-Schreger bands' (HSBs) (Korvenkontio, 1934). Complexly interwoven bundles of prisms that are not arranged in discrete layers are called 'irregular enamel' (Koenigswald and Clemens, 1992; Koenigswald, 1997) and prisms with a strong lateral deviation relative to the enamel surface are termed 'tangential enamel' (Koenigswald, 1977). The three-dimensional arrangement of different enamel types within a tooth define its 'schmelzmuster' (Koenigswald, 1980) and the variation of *schmelzmuster* from tooth to tooth defines the 'dentition' level of the enamel microstructure hierarchy.

The enamel microstructure of rodent incisors is quite different from that of their molars due to their special functional requirements (Koenigswald *et al.*, 1987, 1994). Rodent incisors are ever-growing, and their main function is to cut and dig. In the majority of rodents, incisor enamel, which covers only the labial portion, is made up of outer radial enamel and inner HSBs oriented transversely to the long axis. Usually HSBs occupy at least 50% of the

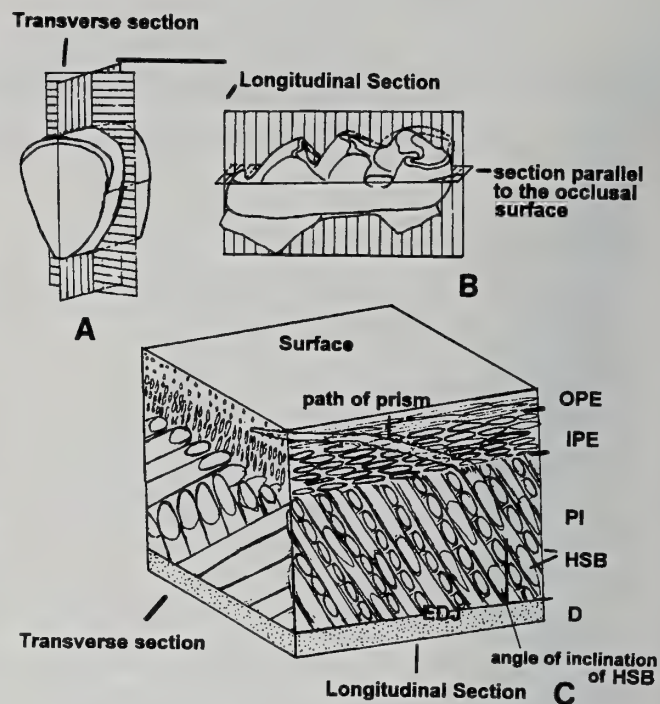
enamel thickness of rodent incisors, but in murid and many caviomorph rodents HSBs can occupy up to 80% (Martin, 1992). The thickness of individual bands of prisms also differs among taxa. A uniserial HSB is 1-2 prism thick, pauciserial 2-4 prisms thick, and multiserial more than 4 prisms thick (Korvenkontio, 1934; Martin, 1993). Murid rodents have only uniserial HSBs.

The main objectives of the present work are 1) to document the complexity of the enamel microstructure in some of the Plio-Pleistocene murids and their extant counterparts collected from India, and 2) to trace the functional adaptation back in time based on comparison of fossil and Recent forms. There are certain morphological characters (such as hypsodonty, relative width of molars and orientation of transverse crests) in murid molars which can be correlated with a grazing diet (Crabb, 1976; Meulen and Musser, 1999). This grazing property of mammalian molars is also reflected at the enamel microstructure level (Rensberger, 1973 1975; Pfretzchner, 1994; Janis, 1988; Fortelius, 1985; Weijs, 1994). Therefore, an attempt has been made here to discover the dietary adaptations (grazing or browsing) of extinct murids from their schmelzmuster, a determination which has important implications for palaeoclimatic reconstruction.

### Material and methods

Specimens examined include fossil and Recent murid rodents housed at the Vertebrate Palaeontology Laboratory, Centre of Advanced Study in Geology, Panjab University, Chandigarh, India; around one hundred Recent mice specimens were provided by T. Sharma, BHU, Varanasi, India and *Megacricetodon* specimens were provided by T. Bolliger, Palaeontological Institute, Zurich.

Genus: *Mus*. Species: *M. booduga*, *M. dunni*, *M. musculus musculus*, *M. m. domesticus*, *M. m. tytelri*, *M. saxicola*, *M. flynni*, *M. linnaeusi* and *Mus* sp. Material: Upper and lower first left molars and incisors of *M. m. tytelri* (specimen numbers HMD-13, 12, 5, 10, 6, 9, MMt-1&4); *M. m. musculus* (MMC1, 2, 3 from Czechoslovakia, Mdwsb 4, 5 WSB strain European, HMV-4, 6 from Varanasi); *M. musculus bactrianus* (JP-2, 3, 4 house mouse from Jodhpur); *M. m. castaneus* (NKM-20 from Kathmandu, Nepal; HMNG-2, house mouse from Narpat Ganj, HMMD, from Madras, HMMM-3 from Mysore, HMGW-1, 3, 8, 9, HMGI-1, 3 from Gangtok wild and indoors respectively); *M. booduga* *M. dunni* (MBV-1, 2, 3 from Varanasi MBY-1, 3, 4 from Mysore, MDV3, 1-Type I, MDM5, 6-Type II, MDM1, 3-Type III); *M. saxicola* (upper molar and lower incisor, MS-33); *M. flynni* (upper and lower incisors and first molars, MFI-1, 2, MFM-1, 2, SM-6, 25, Late Pliocene Siwaliks around 2.5 m.y.); *M. linnaeusi* (lower jaw,



**Figure 1.** Schematic diagram showing sections in this study. A. Transverse and longitudinal sections of incisor. B. Longitudinal section and section parallel to occlusal surface of molar. C. Model of incisor enamel microstructure showing prism orientation. Abbreviations: D = dentine; EDJ = enamel dentine junction; HSB = Hunter-Schreger bands; PI = portio interna; OPE = outer portio externa; IPE = inner portio externa. PI with HSBs (portio interna with Hunter-Schreger bands) and angle of inclination of HSBs.

VPL/RP-GII, 2 m.y.); *Mus* sp. (upper and lower incisors (MS-1, 2).

Genus: *Bandicota*. Species: *B. sp. cf. B. bengalensis*, *B. indica*, *B. sivalensis*. Material: *B. sp. cf. B. bengalensis* incisors from Pleistocene Narmada valley deposits. *B. sivalensis* upper jaw (VPL/RP-SM-78) from Tatrot Formation (Late Pliocene). *B. indica* (extant form).

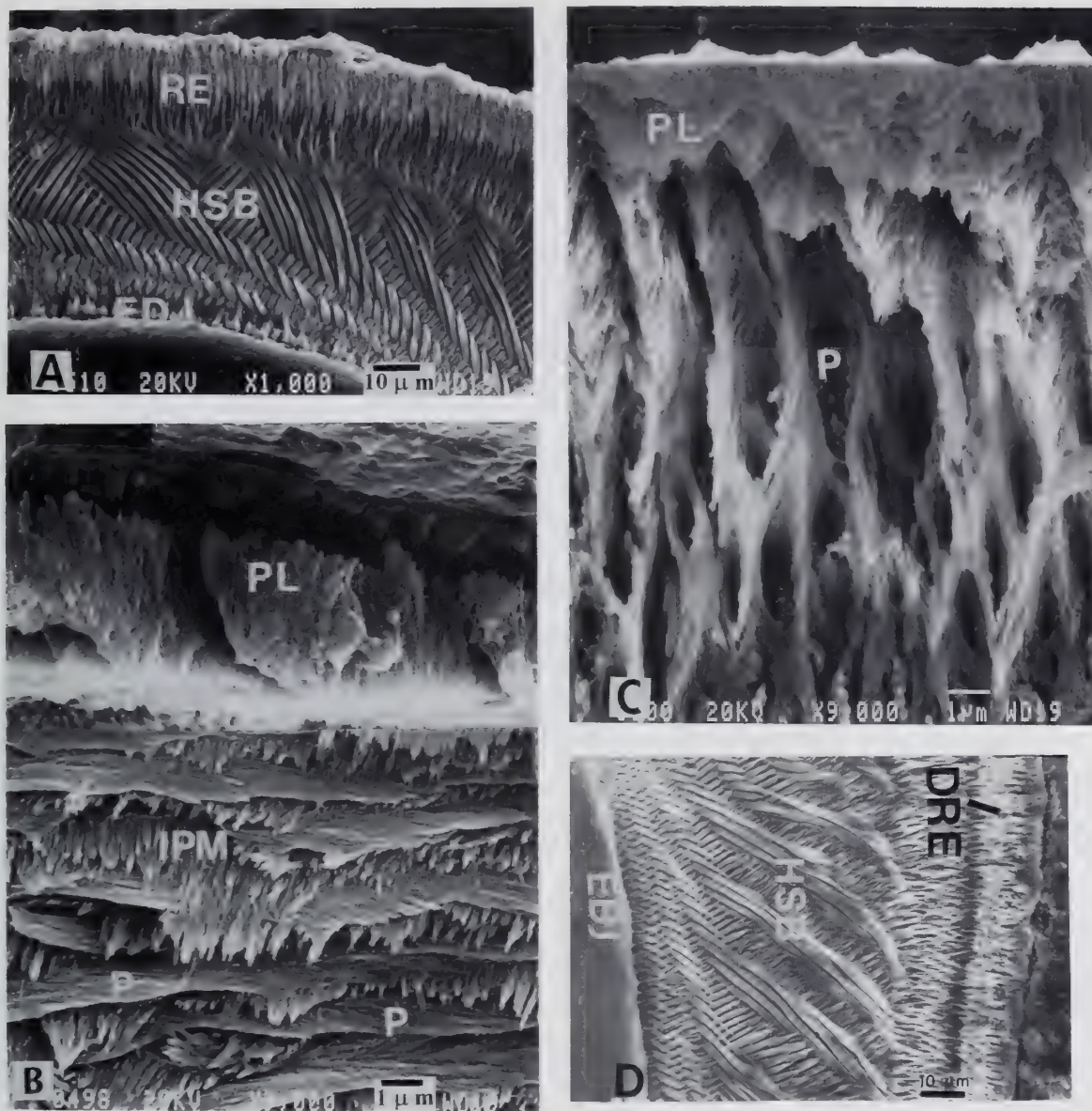
Genus: *Golunda*. Species: *G. tatroticus*, *G. kelleri*, *G. sp.*, *G. ellioti*. Material: Upper and lower incisors and second lower molar (VPL/RP-M2A).

Genus: *Millardia*. Species: *M. meltada* (extant), cf. *Millardia*. Material: Incisors and molars of the Recent form and those collected from Late Pliocene Siwalik deposits.

Genus: *Parapelomys*. Species: *Parapelomys robertsi*. Material: Lower jaw (VPL/RP-SM-58, Late Pliocene Siwalik deposits). A cricetid, *Megacricetodon gregarius* (15-13 m.y.) from La Grive (France). Fifteen to 20 specimens (including molars and incisors) of each extant species mentioned were studied. In the case of fossil taxa, only a few specimens (2 to 5) were used in the present study.

Isolated fossil incisors were identified by comparisons



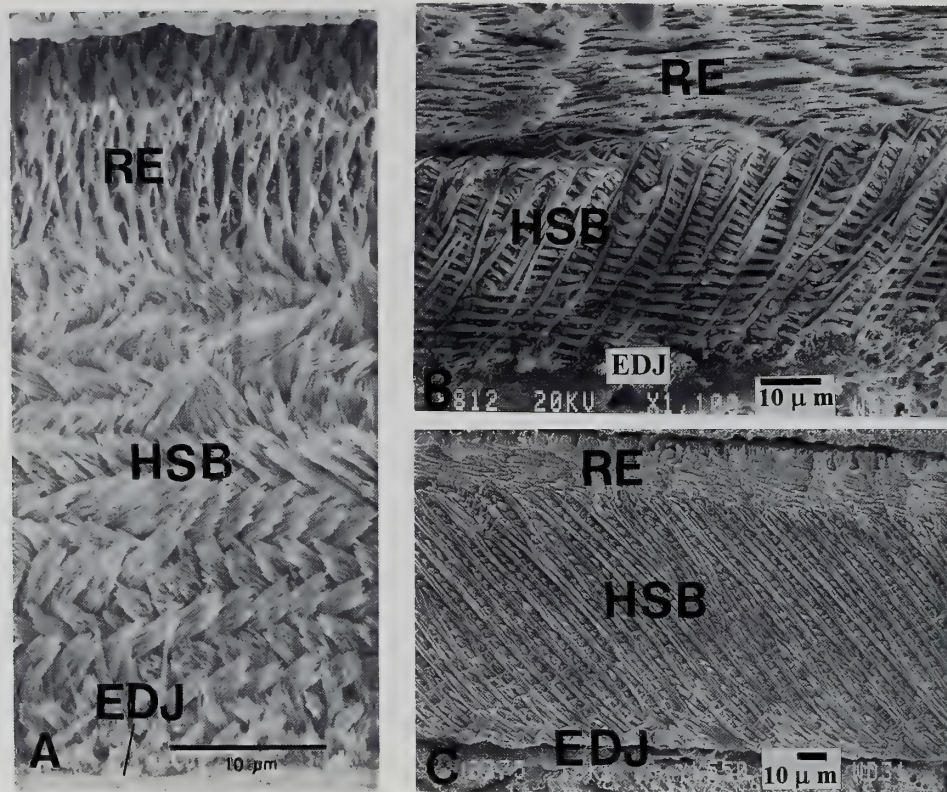


**Figure 2.** Enamel microstructure in the incisors of some extant *Mus*. **A.** Transverse section of upper incisor of *Mus musculus tytelri*. **B.** Longitudinal section of upper incisor (tip on left-hand side) of *Mus musculus tytelri* showing only part of radial enamel. **C.** Outer radial enamel of upper incisor of *Mus musculus tytelri* in transverse section. **D.** Transverse section of upper incisor of *Mus (Pyromys) saxicola*. Abbreviations: PL = plex; P = prism; IPM = interprismatic matrix; other abbreviations as same as in Figure 1.

with those of their closest extant relatives. For enamel microstructure studies, the molars and incisors were embedded in polyester resin. Based on the area of investigation, sections (longitudinal, transverse, tangential and sections parallel to the occlusal surface of the dentition) were made (Figure 1) and studied both under stereoscopic and scanning electron microscopes. Some of the molars were sectioned parallel to the occlusal surface at particular (approximately 0.25–0.5 mm) intervals of depth (serial sectioning method) for mapping of the schmelzmuster (spatial

arrangement of various enamel types in the whole tooth). In order to view the same part of the enamel of the same molar position of different *Mus* species, all the teeth were aligned and oriented inside one slab of polyester resin and sectioned at the same depth. Sections were polished and etched with mild acid, 5% HCl. Mapping of enamel types was carried out initially by using a light microscope and later the polished surfaces were coated with gold in order to study them under the scanning electron microscope (SEM). The scheme proposed by Koenigswald and Clemens (1992)





**Figure 3.** Enamel microstructure in incisors of some fossil *Mus*. **A.** Transverse section of upper incisor of *Mus flynni* (from Late Pliocene Siwalik sediments). **B.** Longitudinal section of upper incisor (tip on right-hand side) of *Mus flynni*. **C.** Longitudinal section of lower incisor (tip on left-hand side) of *Mus flynni*. Abbreviations as same as in Figures 1 and 2.

to study enamel microstructure including various structural complexities and murid dental terminology proposed by Jacobs (1978) has been followed here.

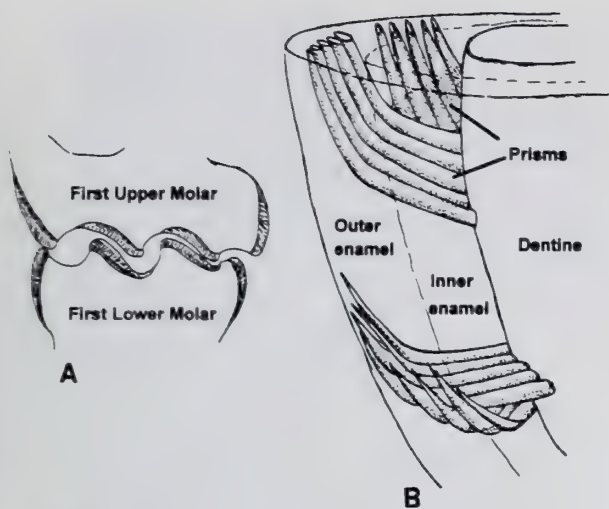
### Observations

Upper incisors of all the *Mus* species studied, including the fossil specimens in transverse section, contain uniserial HSBs (portio interna or inner enamel) that are apically inclined and occupy more than 70% of the total thickness of the enamel layer. The typical uniserial HSBs are arranged transversely to the long axis of the incisor. Outer enamel (portio externa) is divided into two parts: an inner part of radial enamel consisting of apically oriented prisms and vertical IPM, and an outer part consisting of dense prisms and IPM (etched prismless external layer or PLEX) (Figure 2A-D). This differentiation of the portio externa is not found on fossil upper and lower incisors, where the portio externa consists only of radial enamel (Figure 3A-C). Prisms have a lensoid shape in cross section. Crystallites of interprismatic matrix (IPM) run perpendicular to those of prisms, providing a strong interlocking system (Figure 2B).

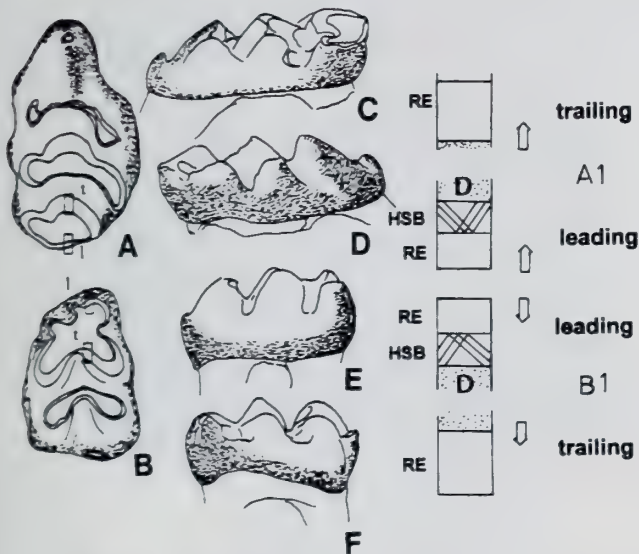
HSBs (portio interna) on lower incisors occupy a greater portion of the enamel and are inclined less steeply than those on the upper incisors. Therefore, in transverse section more bands are encountered on the lower incisors.

On the upper and lower molars of mice, the occlusal surface is covered by occlusally oriented prisms of radial enamel (Figure 4A, B). On leading edges of cusps, these prisms converge with their long axis pointing towards the cutting edge (Figures 5, 6D, 7). On trailing edges, radial enamel with interrow sheets emerges from the EDJ with prisms oriented towards the cutting edge. Often in sections parallel to the occlusal surface or on slightly ground lower molars, HSBs emerging from the EDJ are inclined towards the occlusal surface (Figures 4, 6D, E). As we move towards the base of the molar, they tend to become horizontal and parallel to the occlusal surface (Figures 4, 7A, C, D). At the very base, the HSBs occupy almost the total thickness of the enamel running from the EDJ to the outer part (Figure 7C). Prisms of alternate bands decussate at a high angle and crystallites of IPM are at right angles to those of the prisms (Figure 6E). This layer is followed by radial enamel containing prisms oriented





**Figure 4.** Schematic diagrams showing sections of first upper and lower molars of *Mus musculus*. **A.** Occlusion of first upper and lower molars of *Mus musculus* showing prism orientation. **B.** Model showing prism orientation at tip and base of anterior most cusp on first lower molar.



**Figure 5.** Schematic diagrams of *Mus musculus* first upper and first lower molars. **A.** occlusal; **C.** labial; **D.** lingual views of first upper molar and **B.** occlusal; **E.** labial; **F.** lingual views of first lower molar of *Mus musculus* with approximate distribution of HSBs. Blowups of **A** (**A1**) and **B** (**B1**) showing differentiation of leading and trailing edge. Arrows indicating load direction. Abbreviation same as in Figures 1 and 2.

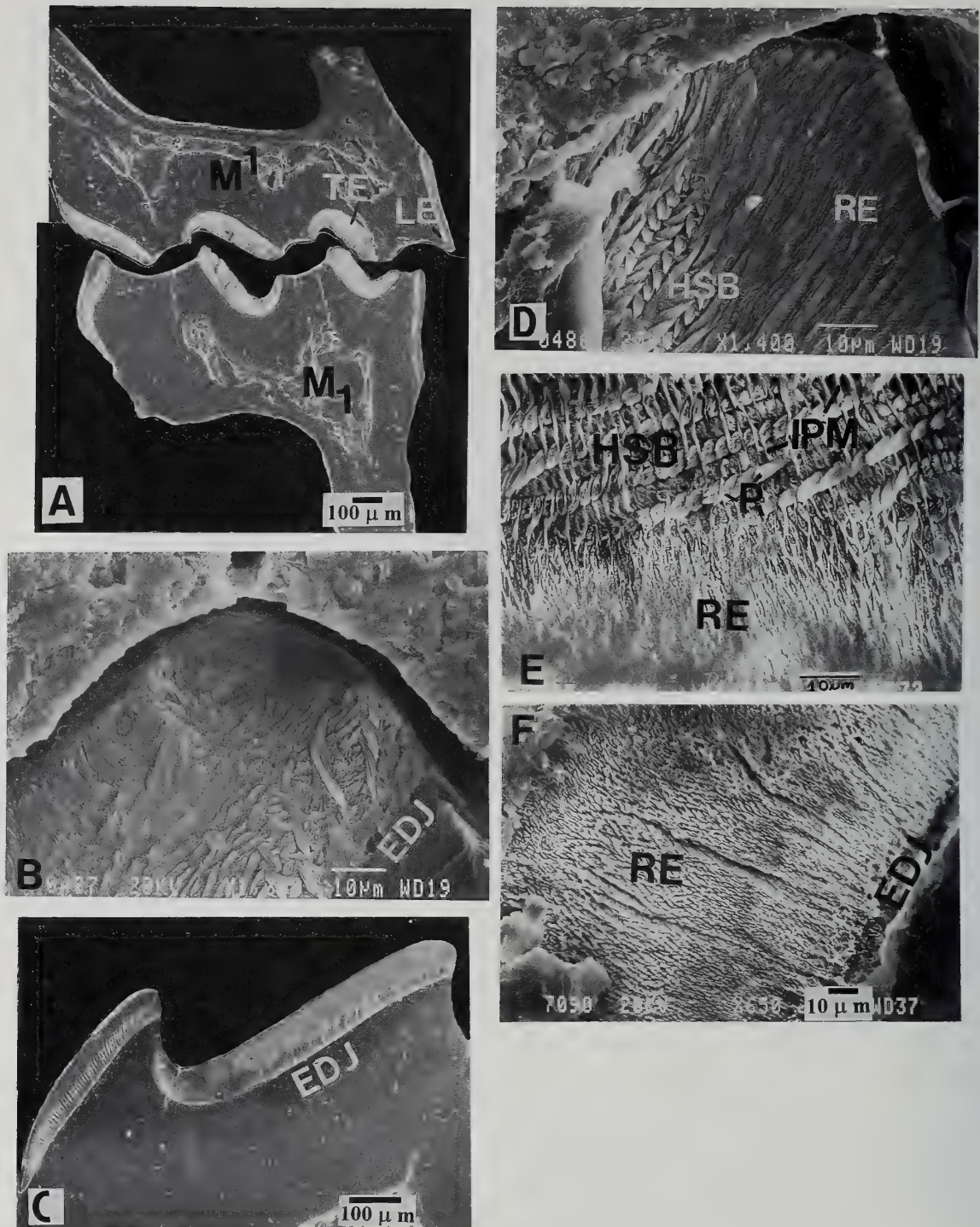
occlusally. In longitudinal sections of upper and lower molars, the HSBs run from the base to the tip of the anterior and posteriormost cusps, a structure similar to that seen on incisors (Figures 6A, 7C, D). These horizontal HSBs are also found on the labial and lingual walls but are con-

centrated around the roots. Therefore, HSBs cover the anterior, posterior and lingual sides of the upper first molars where major roots are found (Figure 5). Enamel on transverse cusps apart from the anterior ones (anterostyle, lingual and labial anterocones on the upper first molars and labial and lingual anteroconids on the lower first molars) and posterior ones (hypocone and metacone on the upper molars and posterior cingulum on the lower) lack HSBs (Figures 6A, B, F, 7B). Where a prestyle is present on the lingual anterocone, HSBs are developed on it, running perpendicular to the cusp axis away from the EDJ (Figure 6C).

Upper and lower molars of fossil mice (Pliocene, Siwaliks) also show HSBs running from the root to the crown (Figure 8A–G). At the base of the tooth these HSBs are horizontal, but near the cap they incline occlusally. In *Megacricetodon gregarius* (from the Middle Miocene deposits of Switzerland) the HSBs occupy more than half (from the root-crown junction) of the upper molar crown (Figure 8H).

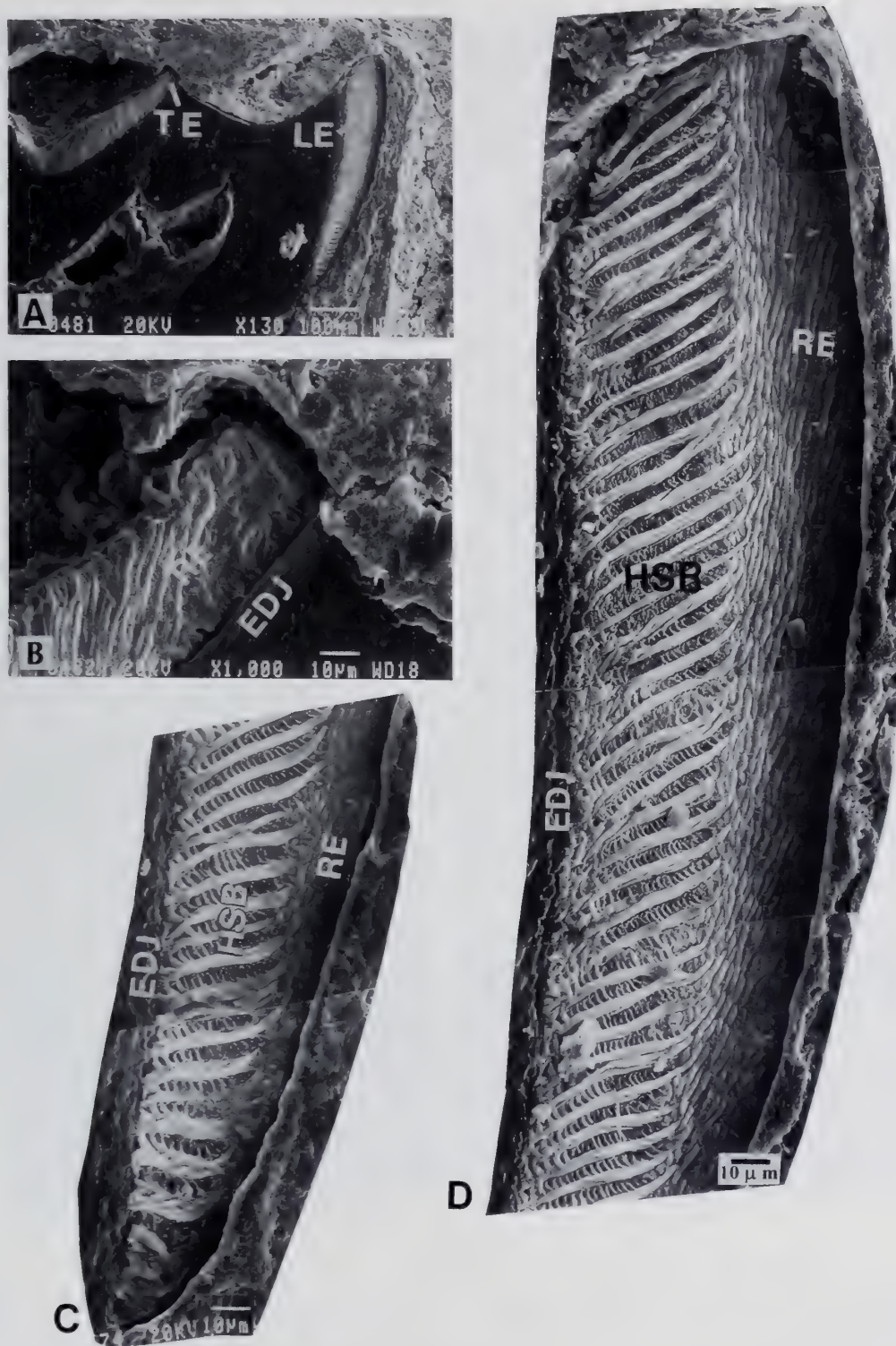
In *Bandicota* sp. cf. *B. bengalensis*, the longitudinal section of the upper incisor shows uniserial HSBs inclined apically at an angle of around 40°. The crystallites of IPM are at right angles to those of the prisms. The prisms of alternate bands decussate at an angle less than 90°. At the EDJ, the IPM crystallites run vertically (relative to the EDJ) and then they change course to run perpendicular to the prisms. At the outer enamel, the crystallites of IPM again become almost vertical as the prisms bend apically. The outer radial enamel is around 25% of the total thickness (Figure 9A). The HSBs of lower incisors are inclined at around 45° to the long axis of the tooth. Prisms of alternating bands decussate very strongly (around 90°). Crystallites of IPM are at a right angle to those of the prisms. The outer radial enamel occupies only 15% of the total thickness. IPM crystallites of the outer enamel run vertically. Prisms of the radial enamel in the lower incisors have a higher inclination towards the outer surface than those of the upper incisors (Figure 10).

On the molars of extant species of *Bandicota*, except for the very minor portion of the base, the entire enamel, including the grinding edges of the occlusal surface, is composed of radial enamel. At the base of the anterior portion the enamel curves beneath the molar and becomes almost parallel to the occlusal surface (Figure 11A). In contrast to incisors, where the outer layer consists of radial enamel and the inner layer of HSB, here the outer enamel contains HSBs and the inner enamel is radial which is modified and appears similar to an interrow sheet (layers of IPM between rows of prisms) (Figure 11B, C). A small portion of the enamel at the base on the posterior margin, which is vertically oriented (relative to the occlusal surface), is also occupied by HSBs (Figure 11E). In the first lower molar the leading and trailing edge differentiation is quite clear



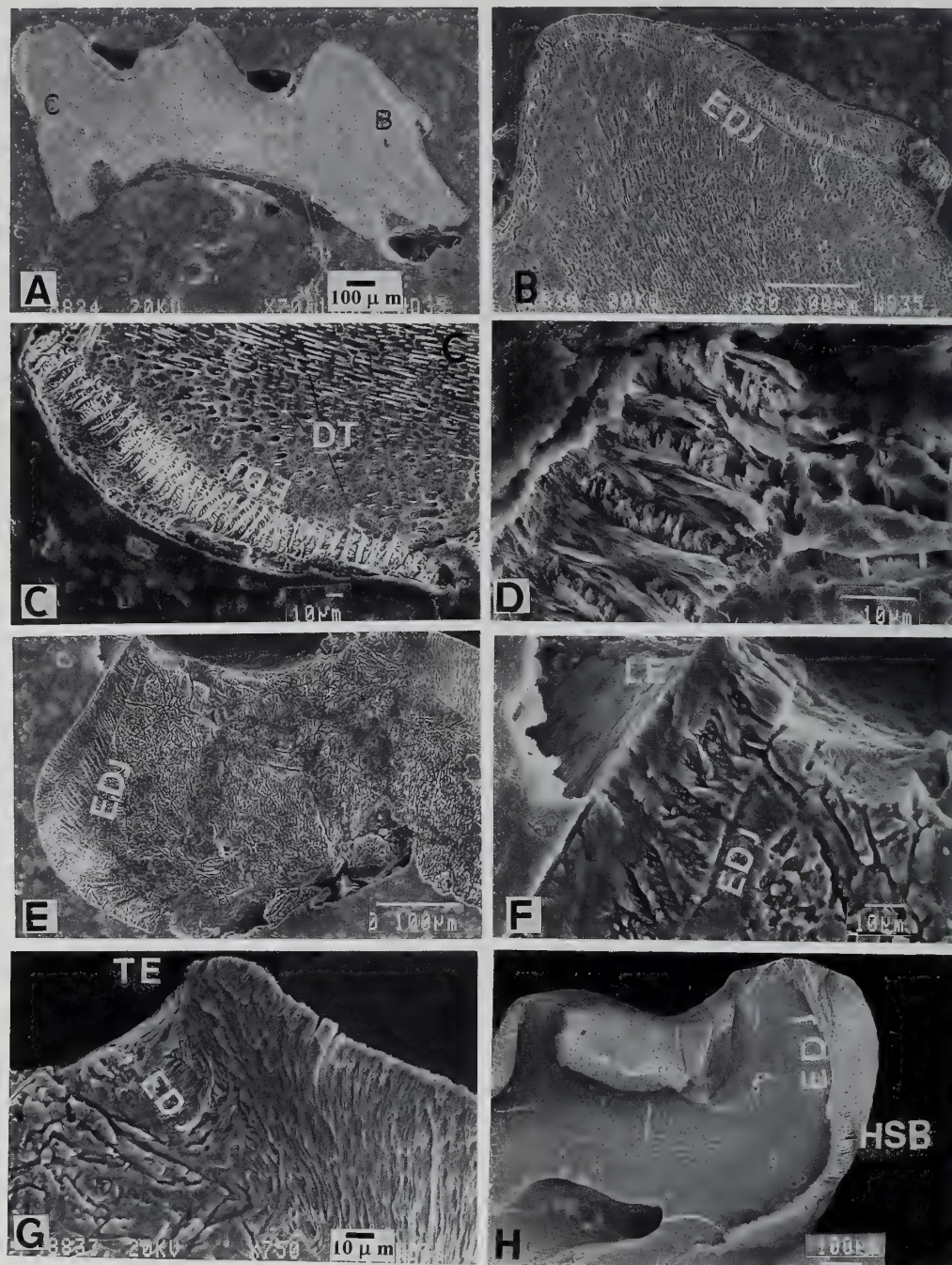
**Figure 6.** Enamel microstructure in molars of some extant *Mus*. **A.** Longitudinal sections of first upper ( $M_1$ ) and lower ( $M_2$ ) molars of *Mus musculus tytelri*. **B.** Trailing edge in longitudinal section of first upper molar of *Mus musculus tytelri* (another specimen). **C.** Longitudinal section of first upper molar of *Mus saxicola* showing prestyle and lingual anterocone. **D.** Longitudinal section of first upper molar of *Mus musculus tytelri* showing leading edge. **E.** Section parallel to occlusal surface of first upper molar of *Mus musculus tytelri*, showing leading edge. **F.** Section parallel to occlusal surface of first upper molar of *Mus musculus tytelri*, showing trailing edge. Abbreviations same as in Figures 1 and 2.





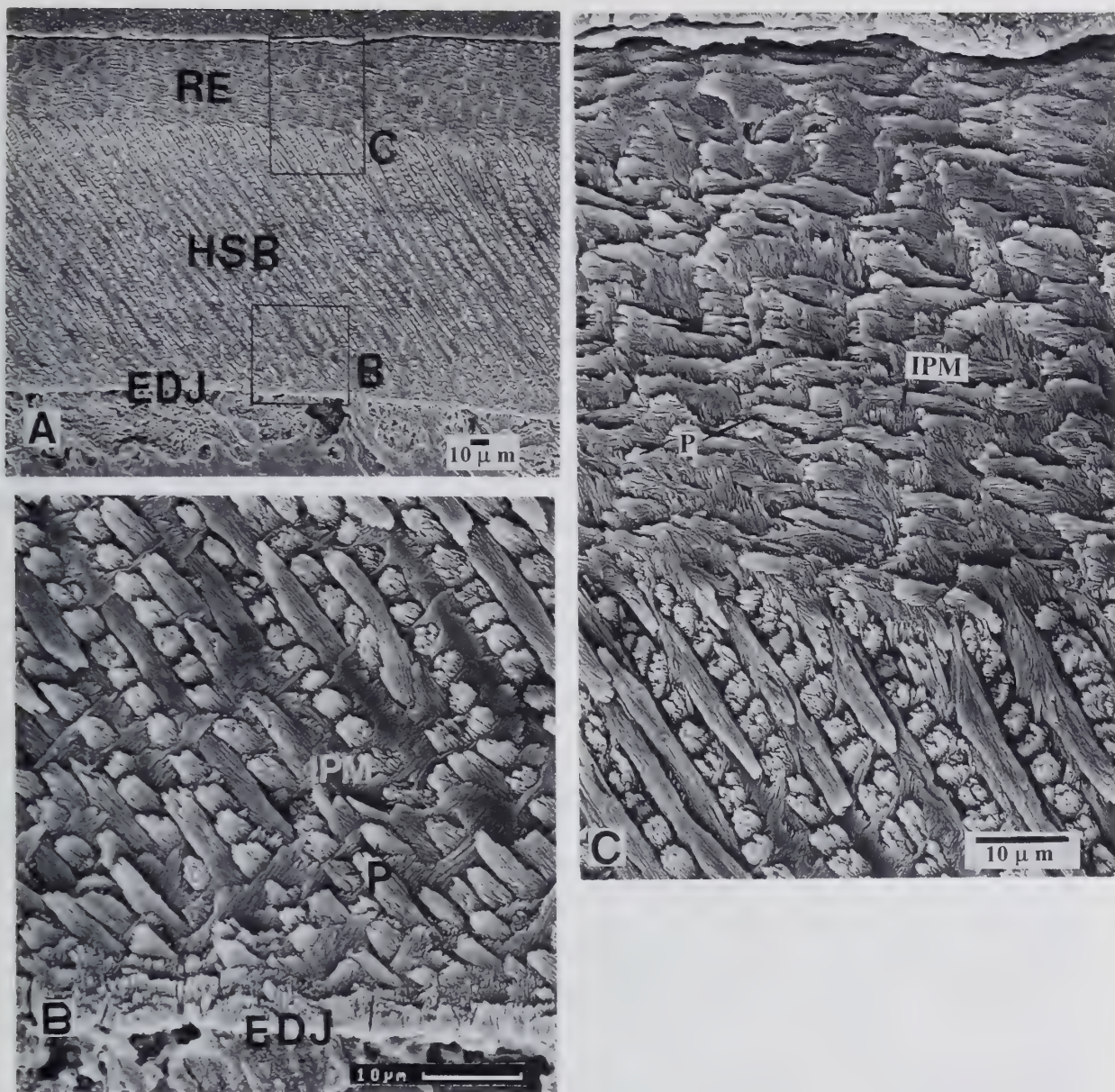
**Figure 7.** Enamel microstructure in first lower molars of *Mus musculus tyelri*. **A.** Longitudinal sections showing anterior part. **B.** Trailing edge in longitudinal section (magnified portion of **A**). **C.** Lower part of leading edge in longitudinal section (magnified portion of **A**). **D.** Upper part of leading edge in longitudinal section (magnified portion of **A**). Abbreviations same as in Figures 1 and 2.





**Figure 8.** Enamel microstructure in molars of some fossil muroid rodents. **A–G.** *Mus flynni* (from Pliocene Siwalik deposits of India). **A.** Longitudinal section of first upper molar of *Mus flynni*. **B.** Anterior part of first upper molar in longitudinal section (magnified portion of **A**, indicated by **B** on **A**). **C.** Posterior part of first upper molar in longitudinal section (magnified portion of **A**, indicated by **C** on **A**). **D.** Tip of posterior part of first upper molar in longitudinal section (magnified portion of **C**). **E.** Anterior part of first lower molar in longitudinal section. **F.** Tip of leading edge in longitudinal section (magnified portion of **E**). **G.** Tip of trailing edge in longitudinal section (magnified portion of **E**). **H.** *Megacricetodon gregarius* (from Miocene deposits at La Grive, France). Oblique section (parallel to probable jaw movement direction) of first upper molar of *Megacricetodon gregarius*. Abbreviations same as in Figures 1 and 2.





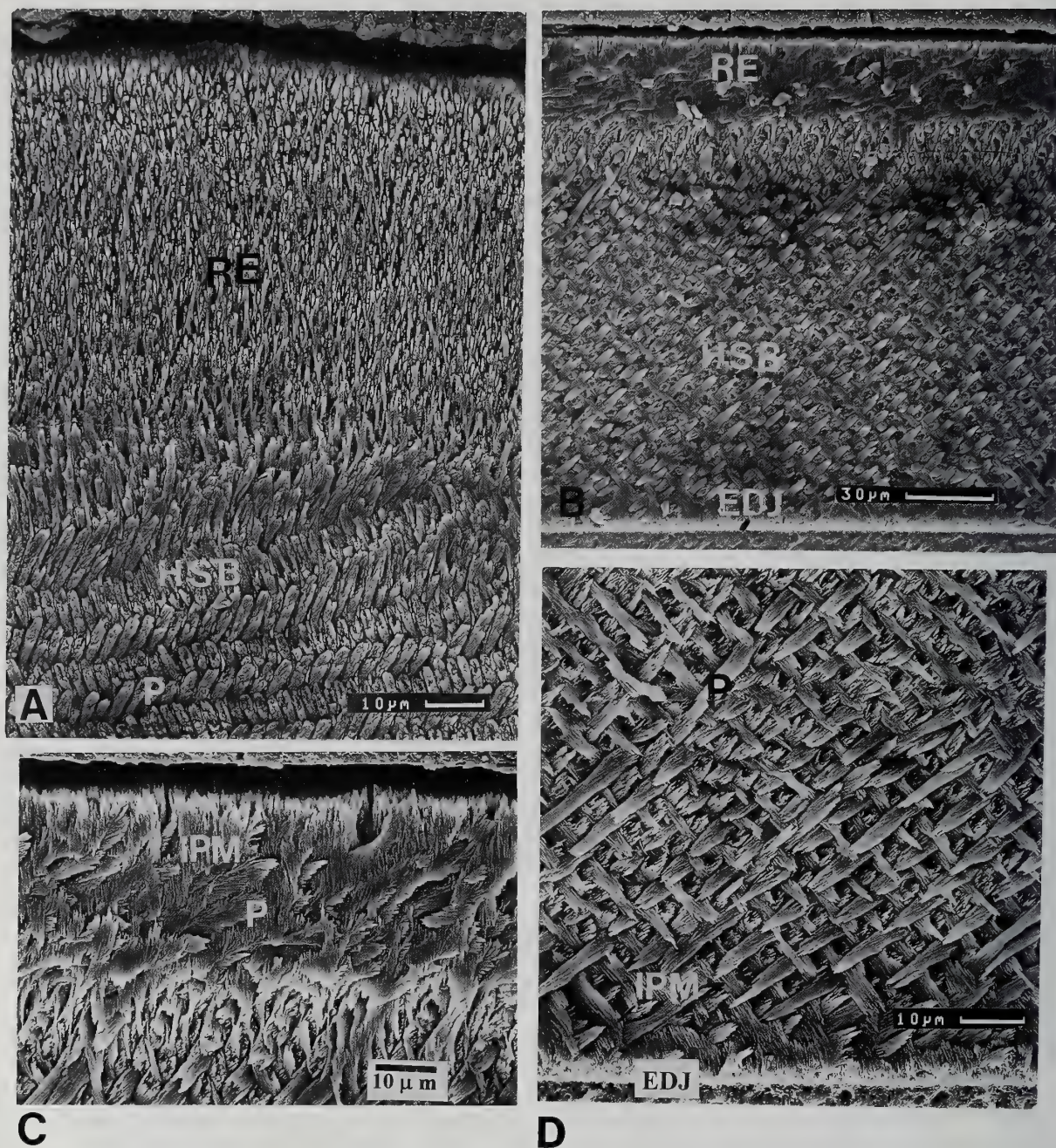
**Figure 9.** Enamel microstructure in upper incisor of *Bandicota* sp. cf. *B. bengalensis* (Upper Pleistocene, Narmada Valley). **A.** Longitudinal section of upper incisor (tip on left-hand side). **B** and **C.** Close-up of lower and upper parts of longitudinal section. Abbreviations same as in Figures 1 and 2.

(Figure 11F, G). Here the prisms in the leading edge originating from the EDJ initially bend forward (their c-axis) occlusally and later turn in the same direction as the load (Figure 11F). Those in the trailing edge run away from the load occlusally (towards the worn surface, Figure 11G). All the species of *Bandicota* studied here show similar patterns.

Upper incisors of *Golunda kelleri* and *G. tatroticus* (fos-

sils) have thick outer enamel (radial enamel) occupying around 30% of the total thickness of enamel (Figure 12A, B). The transversely arranged HSBs are inclined apically by 25°. Prisms of alternate bands decussate at right angles, and the crystallites of IPM are at right angles to the prisms in the third dimension (Figure 12E). HSBs on lower incisors have an inclination of around 35° (Figure 12F).



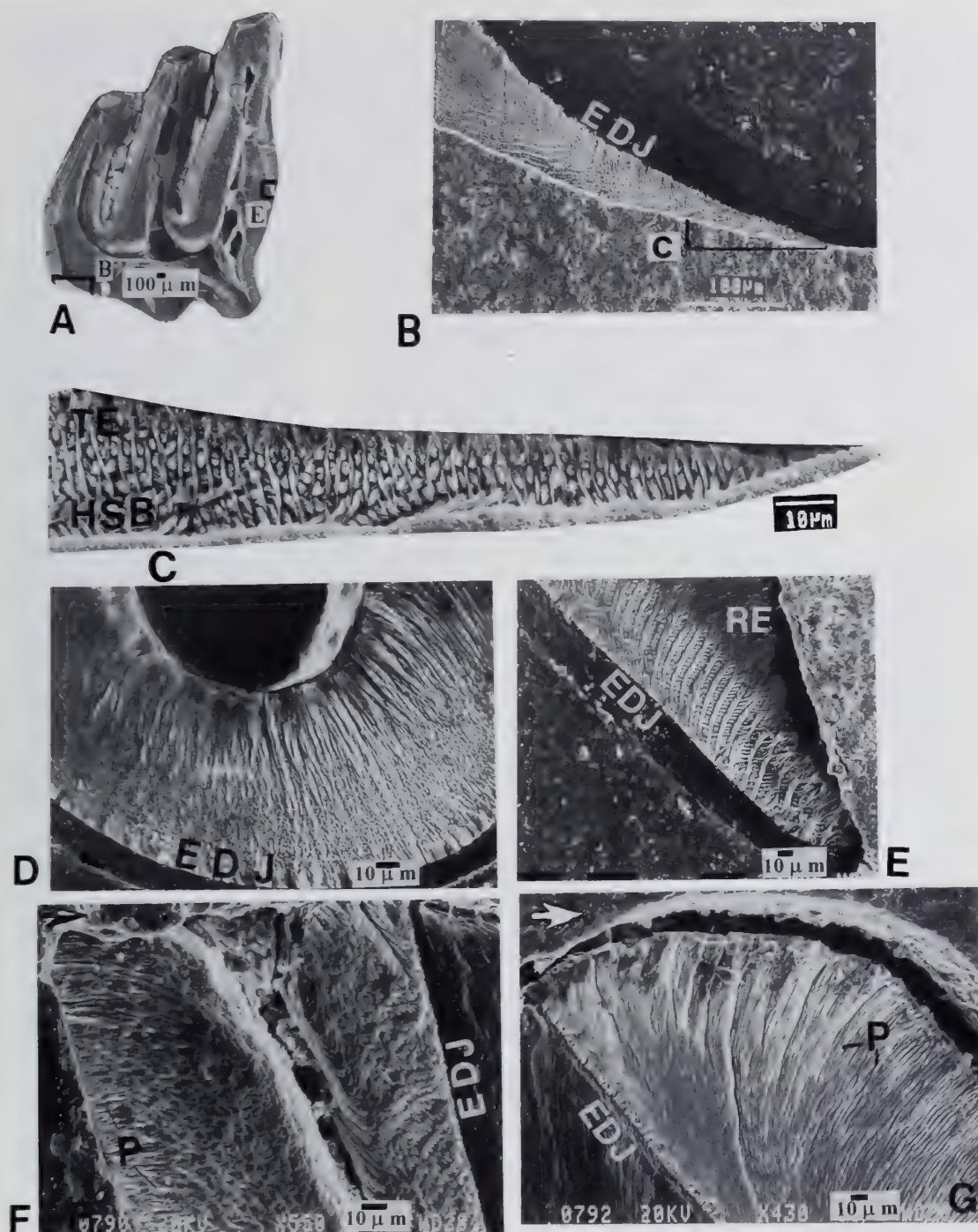


**Figure 10.** Enamel microstructure in incisors of *Bandicota* sp. cf. *B. bengalensis* (Upper Pleistocene Narmada Valley). **A.** Transverse section of upper incisor. **B.** Longitudinal section of lower incisor (tip on right-hand side). **C** and **D.** Upper and lower parts of longitudinal section, close-up of **A** and **B**, respectively. Abbreviations same as in Figures 1 and 2.

Serial sectioning parallel to the occlusal surface on a *G. tatroticus* lower second molar reveals the differentiation of the schmelzmuster at different levels. Slight grinding and etching led to the exposure of the metaconid, which shows presence of radial enamel with interrow sheets at the EDJ with prisms oriented towards the cutting edge. The outer

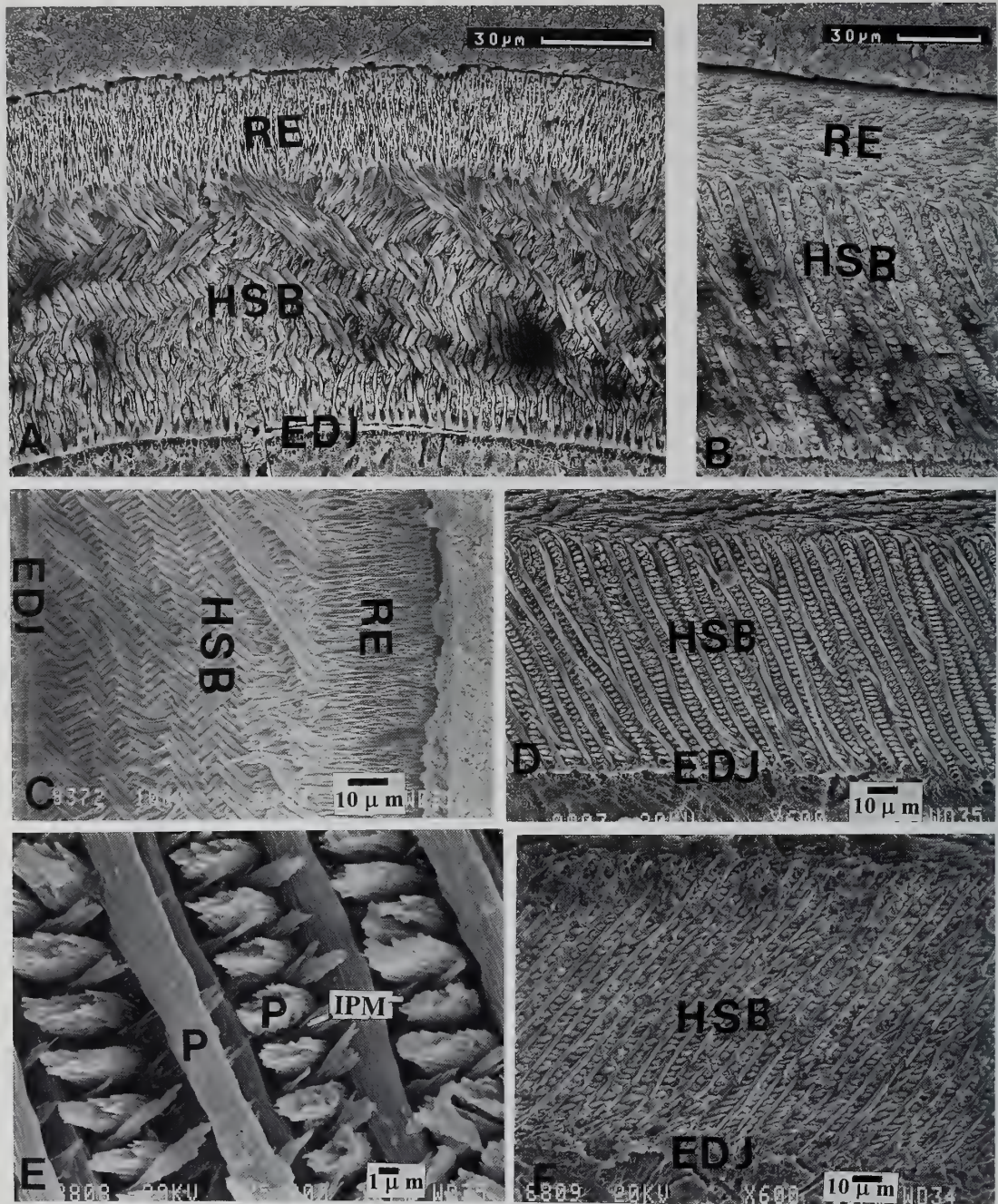
radial enamel has prisms running occlusally at a higher angle (Figure 13A–D). Further grinding reveals the presence of HSBs (Figure 14A–D) with the leading edge having radial enamel on the push (compression) side and HSB on the pull (extension) side (Figure 14A). But the trailing edge of the metaconid still retains the same pattern of radial





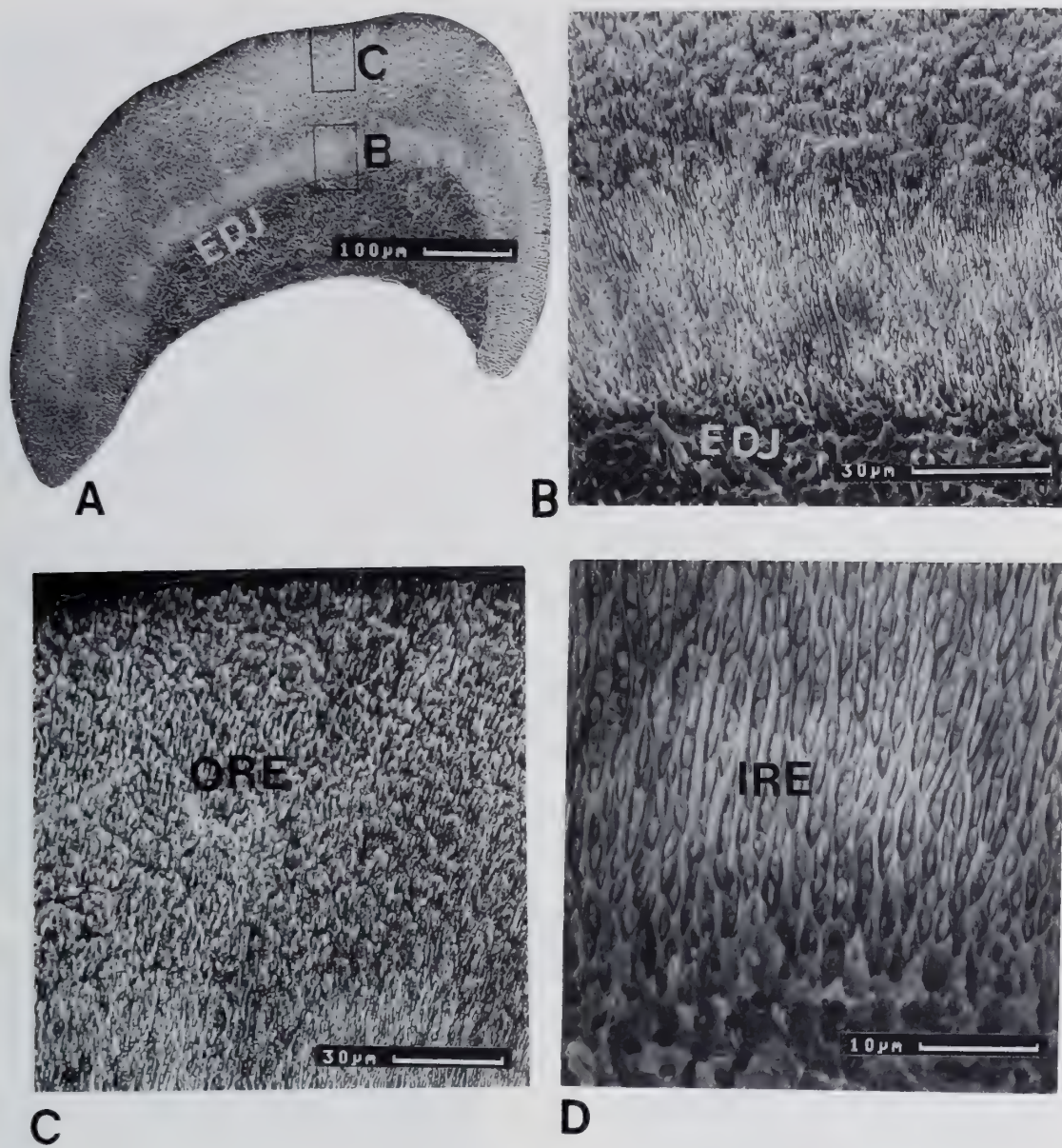
**Figure 11.** Enamel microstructure in molars of *Bandicota bengalensis* as seen in longitudinal section. **A.** Longitudinal section of first upper molar. **B.** HSBs as seen at base of first upper molar (magnified portion of A, indicated by B on A). **C.** HSBs at base of first upper molar, further magnified from a portion on B (indicated by C on B). **D.** Enamel fold as seen on first upper molar (magnified portion of A). **E.** HSBs as seen at posterior end of base of first upper molar (magnified portion of A, indicated by E on A). **F.** Longitudinal section of leading edge of first lower molar. **G.** Longitudinal section of trailing edge of first lower molar. Arrow indicates load direction. Abbreviations same as in Figures 1 and 2.





**Figure 12.** Enamel microstructure in incisors of *Golunda kelleri* and *G. tatroticus*. **A.** Transverse section of upper incisor of *Golunda kelleri* (Late Pliocene Siwaliks). **B.** Longitudinal section of upper incisor (tip on left-hand side) of *Golunda kelleri*. **C.** Transverse section of upper incisor of *Golunda tatroticus* (Late Pliocene Siwaliks). **D.** Longitudinal section of upper incisor (tip on left-hand side) of *Golunda tatroticus*. **E.** HSBs in longitudinal section (magnified portion of HSBs as seen on **D**). **F.** Longitudinal section of lower incisor (tip on right-hand side) of *Golunda tatroticus*. Abbreviations same as in Figures 1 and 2.





**Figure 13.** Enamel microstructure in second lower molar of *Golunda tatroticus*, in sections parallel to occlusal surface. **A.** Enamel microstructure in metaconid (as seen after removal of ~.5 mm of enamel and dentine from occlusal surface). **B.** Inner part of enamel (magnified portion of A). **C.** Outer part of enamel (magnified portion of A). **D.** Radial enamel further magnified from a portion of B. Abbreviations same as in Figures 1 and 2.

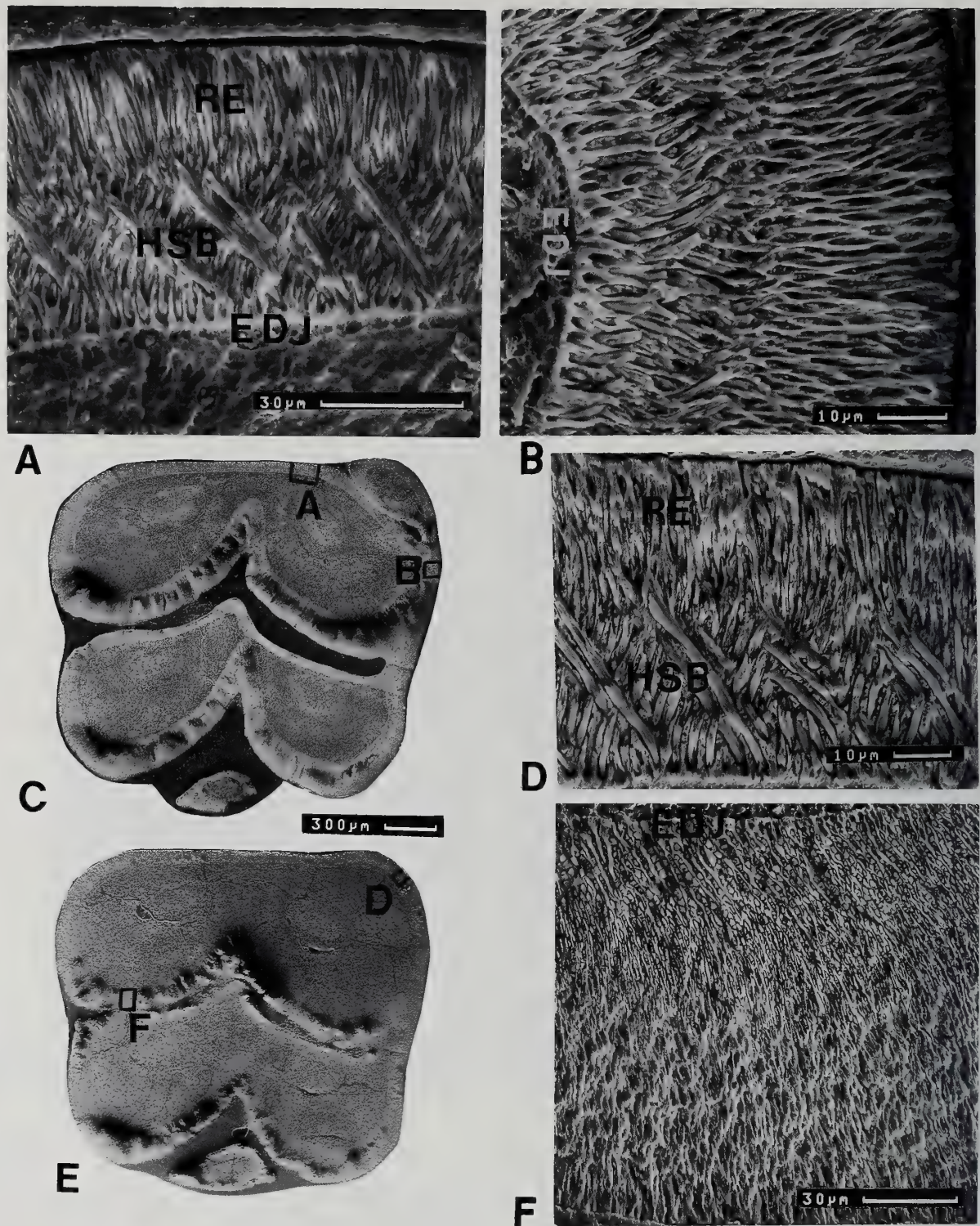
enamel as seen before (Figure 14E, F). At the base of the crown and around the roots, more of the area of the enamel is occupied by horizontal HSBs (Figure 15A–D). The rest of the upper and lower molars show a very similar pattern.

The lower incisor of the extinct *Parapelomys robertsi* shows less inclined HSBs (several bands can be seen) in transverse section (Figure 16E). A very thin outer radial enamel with IPM running vertically (Figure 16F) to the

enamel surface from the EDJ has been observed. As compared to *Golunda*, to which it is closely related (Patnaik, 1997), it has less inclined HSBs.

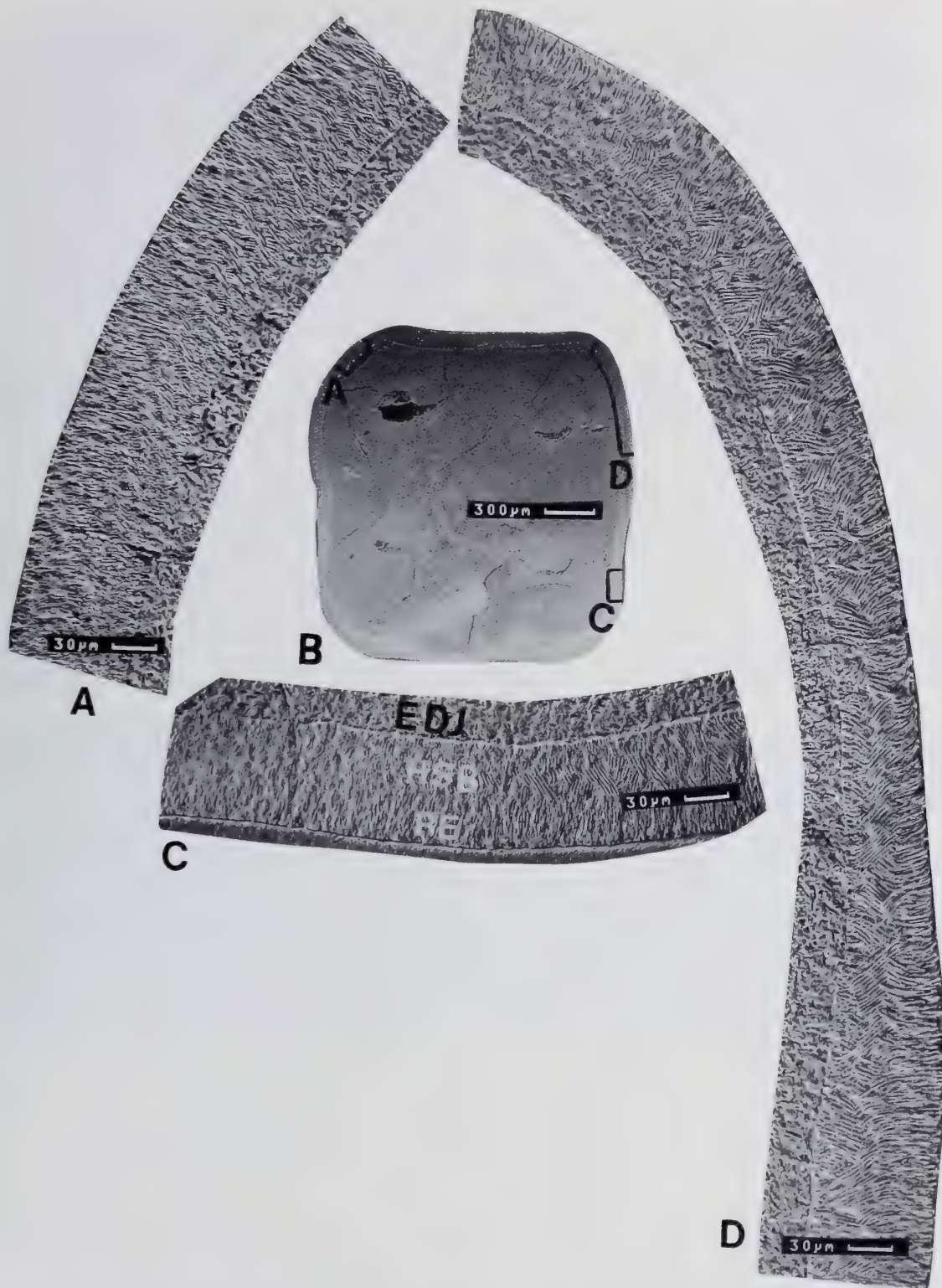
In cf. *Millardia* (from Late Pliocene Siwalik sediments) upper incisors have HSBs apically inclined (50°). A lower incisor of the fossil form (Figure 16D) has thicker outer radial enamel than its extant counterpart, *M. meltada* (Figure 16C). Molars of *Millardia* (both fossil and extant) show a





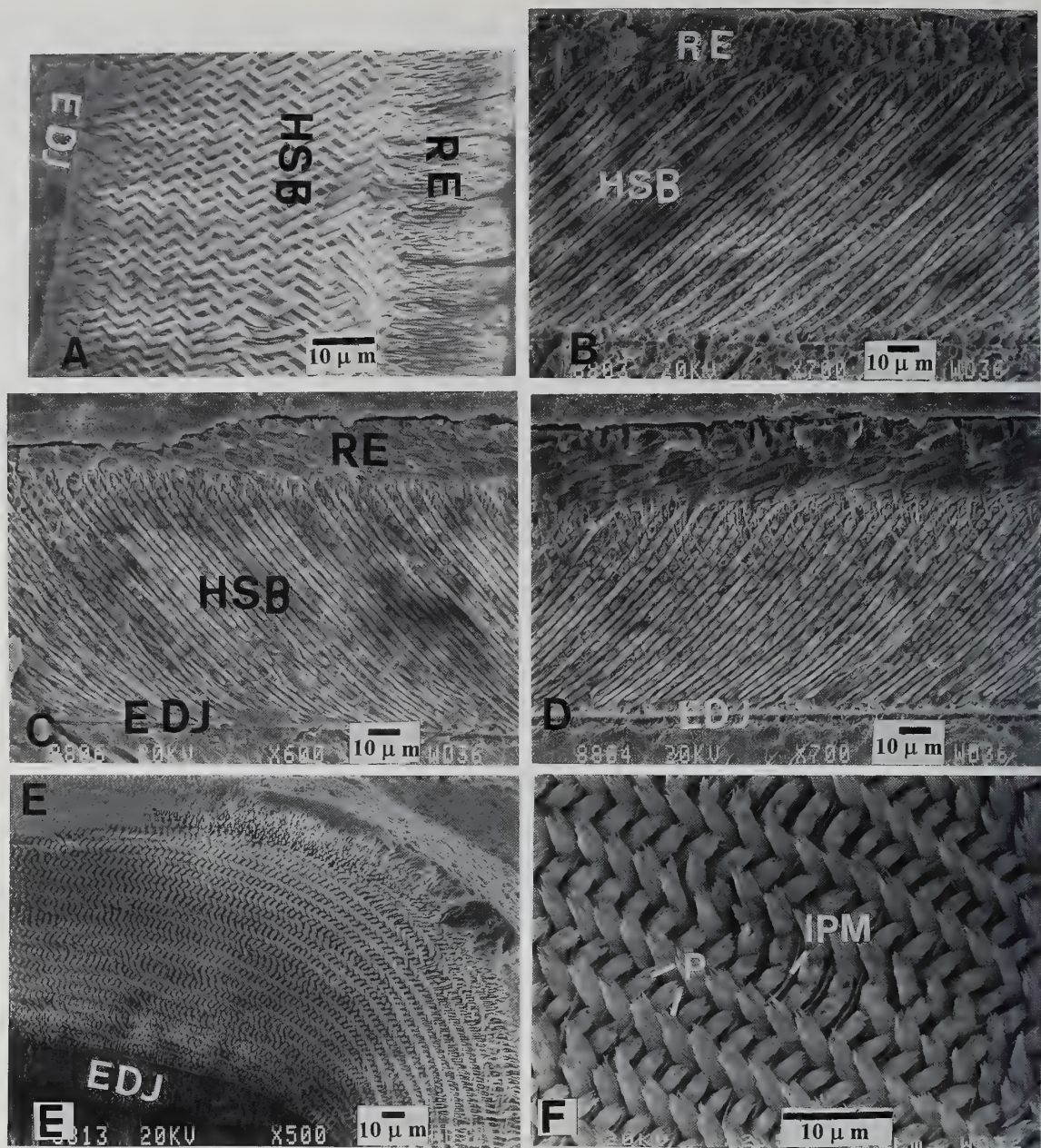
**Figure 14.** Enamel microstructure in second lower molar of *Golunda tatroticus*, sections parallel to occlusal surface. **A.** Magnified part of leading edge (indicated by A on **C**). **B.** Magnified part of labial side (indicated by B on **C**). **C.** Second lower molar. **D.** Magnified part of leading edge (indicated by D on **E**). **E.** Second lower molar, further polished. **F.** Magnified part of trailing edge (indicated by F on **E**). Abbreviations same as in Figures 1 and 2.





**Figure 15.** Enamel microstructure in second lower molar of *Golunda tatroticus*, sections parallel to occlusal surface. **A.** A part of HSBs as seen at base of second lower molar (magnified portion of **B**, indicated by **A** on **B**). **B.** Second lower molar polished up to base. **C** and **D.** HSBs at base of molar (magnified portions of **B**, indicated by **C** and **D** on **B**). Abbreviations same as in Figures 1 and 2.





**Figure 16.** Enamel microstructure in incisors of *Millardia* and *Parapelomys*. **A.** Transverse section of upper incisor of cf. *Millardia*. **B.** Longitudinal section of upper incisor (tip on right-hand side) of cf. *Millardia*. **C.** Longitudinal section of lower incisor (tip on left-hand side) of *Millardia meltada*. **D.** Longitudinal section of lower incisor (tip on right-hand side) of cf. *Millardia*. **E.** Transverse section of lower incisor of *Parapelomys robertsi*. **F.** HSBs, further magnified from **E**. Abbreviation same as in Figures 1 and 2.

very similar structure to that of *Golunda*, i.e., the lower half of the crown contains inner HSBs and outer radial enamel, and the rest of the crown is occupied by radial enamel.

### Discussion

The outer prismless enamel found in all the extant *Mus*

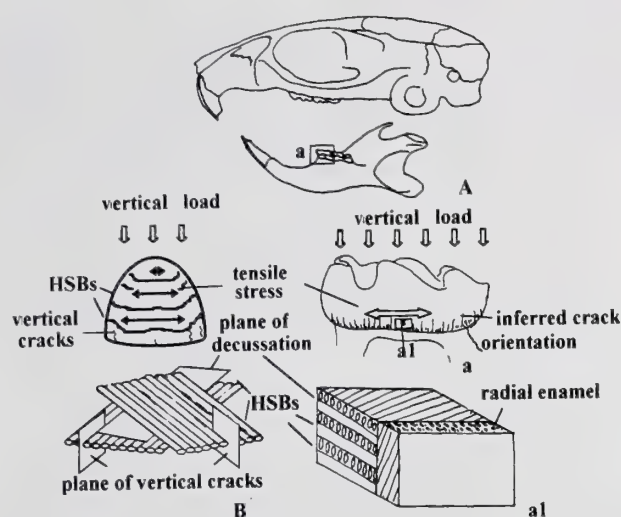
incisors studied here seems to be an etching artifact that could have been produced due to a slight compositional difference between inner and outer radial enamel. Presence of dense outer radial enamel underlain by inner radial enamel and HSBs (which are less resistant to abrasive forces) may facilitate the maintenance of a sharp incisor.

This is the first report of brachydont rodent molars show-



ing HSBs running from the base to the occlusal surface, although on the lingual and labial walls, HSBs occupy only a part of the crown height from the base. Prior to this study only hypsodont and rootless rodent molars have been found to show HSB extending from the base to the top of the crown (Koenigswald, 1980; Koenigswald *et al.*, 1994), although the presence of lamellar enamel with uniserial HSBs covering the base of brachydont molars, such as that of *Cricetus cricetus*, has been noted earlier (Koenigswald and Clemens, 1992; Koenigswald, 1993). Models of stress distribution and prism orientation suggest that horizontal HSBs surround the low-crowned molars in order to provide reinforcement against vertical load and crack propagation (Koenigswald *et al.*, 1987; Pfretzschner, 1988; Pfretzschner, 1994). According to this model, vertical loads on the occlusal surfaces of the upper and lower teeth of mice (Figure 17A) produce horizontal tension in the enamel, which would be at a maximum at the base around the roots. These tensile stresses may lead to expansion of vertical cracks around the walls of the molars. As radial enamel with prisms oriented in one direction is vulnerable to these crack-generating forces, reinforcement of the structure with horizontal HSBs surrounding the base of the molars would inhibit such a development (a1 in Figure 17). It is possible that the HSBs are developed at the base of the crown to reinforce the thin enamel. But if we look at the HSBs in *Mus* (Figure 7), where they occupy the entire enamel crown of varying thickness, this conjecture does not hold strongly. Another example supporting this view is that of *Megacricetodon*, which has molar enamel comparable in thickness to that of mice, but in which the HSBs occupy only half of the crown height (Figure 8H).

In mice, the effective jaw movement is 'proal' (forward stroke). Except for the posterior portion of the hypocone, all the cusps of the first upper molar point their arcuate and concave end posteriorly. In contrast, except for the anterior portions of the lingual and labial anteroconids on the first lower molar, all the cusps of lower molars point anteriorly. During occlusion, the valleys between lingual and medial cusps and those between the medial and labial cusps of the first upper molars are occupied by the lingual and labial rows of cusps of the first lower molars, respectively. The row containing the hypoconid and the entoconid occupies the space between the second and last row of the first upper molar. During a proal jaw movement with the lower jaw moving forward, sharp cutting edges are formed at the anterior margin by lingual and labial anteroconids. The cutting edge formed in this manner on the molars shows a resemblance to the cutting edge of an incisor, where one can see prisms with their long axis pointing towards the occlusal surface in the outer radial enamel and HSBs inclined apically in the inner part of the enamel. Such cutting edges are also formed at the poste-

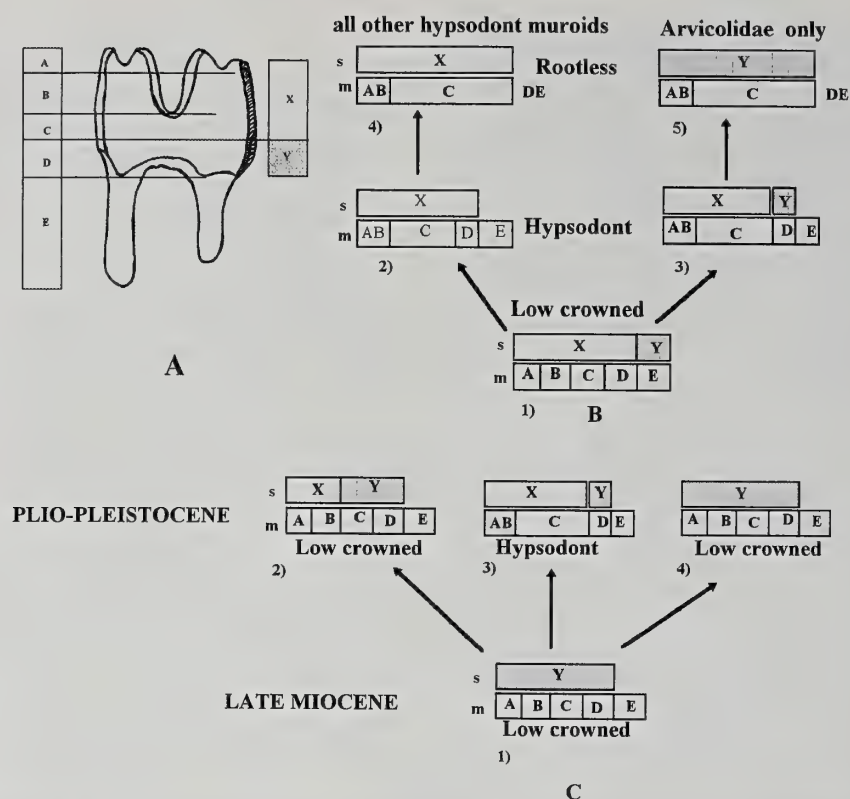


**Figure 17.** Hypothetical schematic diagram, showing arrangement of HSBs in response to vertical load in molars of mice. **A.** Sketches of skull and lower jaw of mice; **a**, first lower molar enlarged; **a1**, schematic model of portion of enamel at base of crown. **B.** Generalised model showing orientation of HSBs, plane of decussation and plane of vertical cracks in response to vertical load on low-crowned molar (adapted from Pfretzschner, 1988).

rior end of the first upper and lower molars. The cusps and valleys that contain outer radial enamel and inner radial enamel with very thick interrow sheets are resistant to abrasion and may help to grind efficiently when in contact.

Differentiation of the leading and trailing edges of enamel microstructure previously has been observed only in hypsodont rodent molars (both with and without roots). In rodents, hypsodonty has led to lamination of the cusps rows, which has simplified the morphology. In hypsodont rodents the radial enamel has invariably been found on the push sides of the cutting edges (Koenigswald, 1980; Koenigswald *et al.*, 1994). This study shows that the brachydont cuspidate dentition in mice also exhibits such differentiation between leading- and trailing -edge enamel. It is even more conspicuous in heavily worn dentitions where cusps are lost and only enamel folds remain. The presence of radial enamel on the push sides of the leading and trailing edges in mice molars justifies their (radial enamel) abrasion-resisting properties. The cutting and grinding ability of mice molars reflects a rather omnivorous diet, which may include browsing shrubs, eating insects and grazing grasses (Dieterlen, 1972).

In hypsodont *Bandicota*, horizontal HSBs probably serve as a crack-stopping mechanism. These horizontal HSBs have been noticed in both vertically and parallelly oriented enamel relative to the occlusal surface. This may indicate that regardless of the orientation of the enamel, horizontal HSBs are present to counter vertical forces. Also noted is



**Figure 18.** Relationship of molar morphology and schmelzmuster in some muroid rodents. **A.** Ontogenetic phases of morphology and schmelzmuster of low-crowned muroid molars. **B.** Difference in heterochrony of morphology (m) and schmelzmuster (s) during evolution from low-crowned (1) to hypsodont (2 and 3) and rootless (4 and 5) molars of muroid rodents. **A** and **B** adapted from Koenigswald (1993). **C.** 1) Low-crowned Late Miocene murids with dominant Y phase (pattern similar to that of *Mus*); 2) Plio-Pleistocene murids such as *Golunda* and *Millardia* with both X and Y phases equally developed; 3) Plio-Pleistocene murids such as *Bandicota* with Y phase reduced and X phase considerably prolonged; 4) Plio-Pleistocene murids such as *Mus*, with dominant Y phase. Explanation of various phases in molar morphology and schmelzmuster: **A** and **B**, formation of occlusal surface; **C**, formation of side walls; **D**, formation of base of crown; **E**, formation of roots; **X**, upper part with radial enamel; **Y**, circumferential band of lamellar enamel at crown base.

that the development of HSBs takes place from the radial enamel (Koenigswald *et al.*, 1987). Presence of radial enamel (with prisms in leading edges pointing their long axes towards the load) on the occlusal surface would help in resisting abrasion. This feature suggests an adaptation for an abrasive diet.

In brachydont *Golunda* molars, radial enamel is dominant on the occlusal surface. Only after considerable abrasion can one observe differentiation of leading and trailing edges. Radial enamel is found on the push side and HSBs on the pull side of the leading edge. Radial enamel with interrow sheets has been noticed on the push side and radial enamel on the pull side of the trailing edge. Again presence of horizontal HSBs at the base probably strengthens the tooth against progress of vertical cracks. The predominant radial enamel on the occlusal surface points towards a grazing habit.

Koenigswald (1993) studied the evolution of schmelzmuster in molars of low-crowned and hypsodont rodents

(both with and without roots) from the perspective of heterochrony. He argued that low-crowned molars of muroid rodents with a large portion of their crown occupied by radial and a smaller portion by lamellar (uniserial HSB) enamel evolved into hypsodont molars either lacking lamellar enamel altogether (e.g., *Microtia magna*) and/or retaining this small amount of lamellar enamel on the other (e.g., *Nesokia indica*). He observed that in rootless hypsodont molars the radial enamel extends from the base to the top in some species (e.g., gerbil, *Rhombomys opimus*) and that lamellar plus radial enamel extends from the base to the top in others (e.g., arvicolids). Further, he suggested that, in most muroid rodents (except for arvicolids), morphology and schmelzmuster follow the same heterochronic modifications. The base of a low-crowned cricetid molar has lamellar (uniserial HSBs) and radial enamel occupying the inner and outer enamel, respectively (Figures 18A, the 'Y' phase, corresponding to D phase of morphology). The rest of the crown of a cricetid



molar is occupied by radial enamel (Figure 18 A, the 'X' phase, corresponding to A, B and C phases of morphology). According to Koenigswald (1993), the structure seen on low-crowned cricetids gave rise to those observed on hypsodont and rootless muroid rodents; 1) with the entire crown occupied by the 'X' phase and 2) with the entire crown occupied by 'Y' phase (arviculids). In arviculids, acquisition of the 'X' phase is accelerated and gives way to the 'Y' phase (Figure 18B).

In the context of the present observations, the heterochrony hypothesis of Koenigswald (1993) is not strongly supported for murids, although it could still be applicable to other muroids, for example, cricetids and arviculids. In the Indian murids, the 'Y' phase in brachydont mice occupies the whole crown (Figure 18C, 1). Taking into account the temporal and spatial distribution of this structure it is suggested here that this should be regarded as the basic structure for the family Muridae. It extends up to the Recent with the *Progonomys-Mus* lineage. *Mus* originated from *Progonomys* in the Late Miocene (around 5.7 m.y. ago, Jacobs and Downs, 1994). In fact, *Progonomys*, which had a wide distribution during the Miocene (Indo-Pakistan, China, Africa, Europe), is the basic stock that gave rise to all the fossil and extant murids, which includes more than 500 extant species and 120 genera. In contrast to the *Mus* pattern, where the 'Y' phase dominates, brachydont *Golunda* and *Millardia*, which are phylogenetically related to the *Karnimata* group (Patnaik, 1997, 2001) of Late Miocene time, have the 'Y' phase restricted to the lower half of the crown and the 'X' phase occupying the rest of the crown (Figure 18C, 4). This structure also extends to the Recent. A different pattern is seen in hypsodont murids. Hypsodonty in murids is first noted in *Dilatomys* of the Pliocene Siwaliks and Late Miocene deposits of Afghanistan (see Sen, 1983; Patnaik, 1997), which appears after the emergence of C4 grasslands in the subcontinent (Cerling *et al.*, 1993). In spite of being hypsodont, cusp patterns of *Dilatomys* are similar to those seen on *Parapelomys-Saidomys* (again related to *Karnimata*) and it has been placed in one group with *Bandicota* and *Hadromys* (Patnaik, 1997). Here, the phase 'X' extends to cover the occlusal surface, and the phase 'Y' is reduced considerably to occupy only a small portion of the base around the roots (Figure 18C, 3).

In this study the genera *Mus*, *Golunda*, *Millardia*, and *Bandicota* can be distinguished broadly by variation in schmelzmuster (angle of inclination of HSBs, percentage of HSBs and RE in incisors; extent of distribution of HSBs and prism orientation in molars, etc.). In the genus *Mus*, it was found that closely related species (here belonging to the subgenus *Mus*) do not show any considerable difference at the microstructural level. However, *Mus* (*Pyromys*)

*saxicola* differs from all the other *Mus* species at the schmelzmuster level, as it shows a slight difference in the shape of the first upper molars (Figure 6C). Nevertheless, it appears that, given similar shape and size of dentition and dietary habits, it is difficult to distinguish closely related species of *Mus* based on enamel microstructure alone.

## Conclusions

1. The molars of *Mus* show some sort of specialisation at the microstructure level by having a kind of 'incisor-like' arrangement of HSBs and radial enamel running from the base to the top of the crown, which could be useful in maintaining sharp cutting edges to break down leaves and insects. In addition to this, the low-crowned *Mus* molars also show grinding ability.
2. Predominance of radial enamel on the occlusal surface of molars of *Golunda*, *Millardia* and *Bandicota* might be indicative of their adaptation for a grassy diet.
3. The results of this paper are in accordance with the hypothesis that the presence of horizontal HSBs counters vertical forces. In *Bandicota*, the HSBs in the enamel are horizontal in spite of the enamel being almost horizontal and parallel to the occlusal surface. Another unique feature of *Bandicota* molars is that HSBs in the enamel layer orientated almost parallel to the occlusal surface occupy the outer part of the enamel whereas the inner part has tangentially oriented radial enamel.
4. For murid rodents a schmelzmuster similar to that of *Mus* should be taken as the basic pattern which could have given rise to patterns similar to the low-crowned *Golunda*/*Millardia* and hypsodont *Bandicota*.

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# Paleobiogeographic significance of *Trominina hokkaidoensis* (Hayasaka and Uozumi) (Gastropoda: Buccinidae) from the basal part of the Tanami Formation (Oligocene) of the Kii Peninsula, southern Japan

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**Abstract.** The basal part of the Tanami Formation, in the southern part of the Kii Peninsula, southwest Honshu, southern Japan, contains elements of the Asagai-Poronai fauna (late Eocene to early Oligocene age) of northern Japan. These include *Malletia poronaica* (Yokoyama), *Portlandia* (*Portlandella*) *watasei* (Kanehara), and *Trominina hokkaidoensis* (Hayasaka and Uozumi). The combination of late Eocene to early Oligocene Asagai-Poronai mollusks and previously known Oligocene to early Miocene mollusks from the Tanami Formation implies that the localities discussed here are of Oligocene age. The presence of *Trominina*, which was widespread in the northern Pacific during Paleogene time, suggests that it migrated from northern Japan and northward to southern Japan, in accordance with the Eocene-Oligocene transition global cooling trend.

**Key words:** migration, mollusks, Paleogene, *Trominina*

## Introduction

The Kumano Group crops out in the southern part of the Kii Peninsula in southwest Honshu, Japan (Figure 1A), and has been assigned to the lower to middle Miocene, on the basis of mollusks and foraminifers (Hisatomi, 1981). However, Katto *et al.* (1976) previously studied mollusks of the Kumano Group in the Tanami area of the Kii Peninsula (Figure 1B) and erected the Tanami and Uematsu Formations (Figure 2), which they assigned to the Oligocene and lower Miocene, respectively, on the basis of mollusks.

The basal part of the Tanami Formation yields many species of the Asagai-Poronai fauna that occurs in the upper Eocene to lower Oligocene of Hokkaido and northeast Honshu, northern Japan (Honda, 1994). The Asagai-Poronai mollusks are *Portlandia* (*Portlandella*) *watasei* (Kanehara), *Ampullina asagaiensis* Makiyama, *Beringius hobetsuensis* (Matsui), *Trominina* cf. *T. ishikariensis* (Hayasaka and Matsui), and *Fulgoraria* cf. *F. (Musashia) antiquior* (Takeda) (Katto and Masuda, 1978).

I obtained numerous, but rather poorly preserved molluscan fossils from low cliffs exposed on a wave-cut terrace at Tanosaki, in the basal part of the Tanami Formation (Figure 1B). These are identified as *Malletia*

*poronaica* (Yokoyama), *Portlandia watasei*, *Acila* (*Acila*) *kiiensis* Masuda and Katto, “*Teredo*” sp., *Turritella* sp., and *Trominina hokkaidoensis* (Hayasaka and Uozumi) (Table 1). *Trominina*, which is one of the earliest evolved buccinid genera, appeared in the region including Sakhalin and Kamchatka during late Eocene time (Titova, 1994). It has been widely recorded from upper Eocene to lower Miocene strata in the North Pacific: Japan, Sakhalin, Kamchatka, the Koryak Upland, Alaska, and Washington (Titova, 1994).

In this paper, I document *T. hokkaidoensis* from the basal part of the Tanami Formation and discuss the paleobiogeographic significance of *Trominina* in Japan, as well as the age of the formation based on mollusks.

## Geological setting

The Tanami Formation largely consists of pale grey, fine-grained sandstone, grey siltstone, and alternating beds of sandstone and siltstone, and is approximately 1500 m thick (Katto *et al.*, 1976). Its basal granule conglomerate, some 30 cm thick, is unconformably underlain by black mudstone of the Eocene to Oligocene Shimotsuyu Formation in the upper part of the Muro Group. The Tanami Formation is in fault contact with the overlying

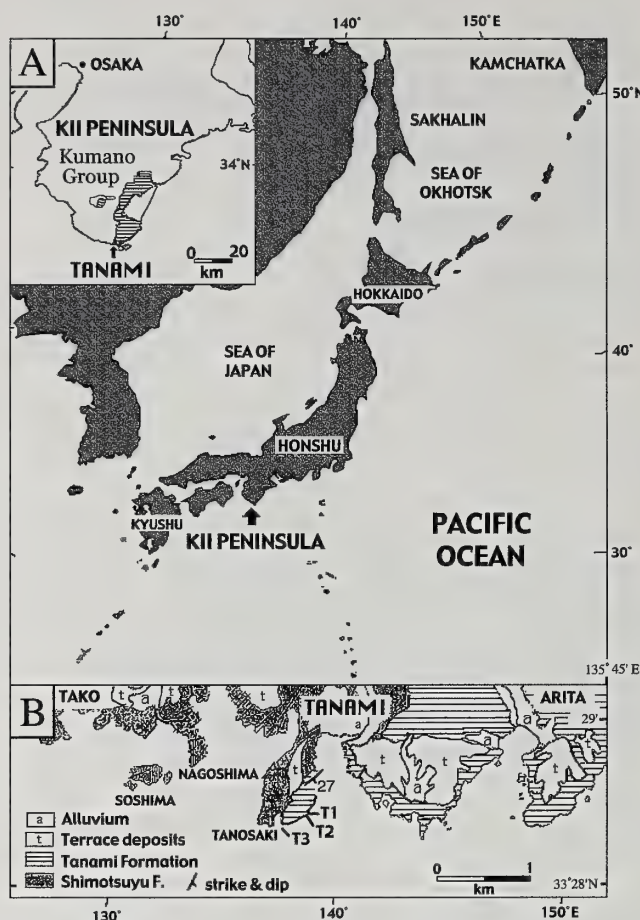


Figure 1. A. Map showing the location of the Kii Peninsula, southwest Honshu, Japan. B. Geologic sketch map of the Tanami area (simplified from Tateishi *et al.*, 1979). T1–T3, fossil localities.

Uematsu Formation (Katto *et al.*, 1976), which contains the Kadonosawa fauna (earliest middle Miocene age; Ogasawara, 2001) (Figure 2).

The upper part of the Muro Group largely contains the Asagai-Poronai fauna, within the Tanami Formation, which includes characteristic elements of this fauna such as *Malletia poronaica*, *Yoldia* (*Yoldia*) *laudabilis* Yokoyama, *Y.* (*Tepidoleda*) *sobrino* Takeda, *Portlandia watasei*, *P.* (*Megayoldia*) *yotsukurensis* Uozumi, *Acila* (*Acila*) *elongata* Nagao and Huzioka, *A.* (*Acila*) *kusiroensis* Nagao and Huzioka, *Cyclocardia akagii* (Kanehara), *C. tokunagai* (Yokoyama), *Orectospira wadana* (Yokoyama), and *Turritella tokunagai* Yokoyama (Mizuno, 1973).

### Discussion

*Trominina* has been recorded from the Paleogene strata bearing the Asagai-Poronai fauna in Hokkaido, northern Japan. Matsui (1957) recorded *T. japonica* (Takeda) from

AGE	HISATOMI (1981)		KATTO <i>ET AL.</i> (1976)		MOLLUSCAN FAUNA
Ma					
	MIDDLE MIOCENE	KUMANO GROUP	MITSUNO FORMATION		KADONOSAWA FAUNA
15			SHIKIYA FORMATION	UEMATSU FM. F	
16					
	EARLY MIO.	KUMANO GROUP	SHIMOSATO FM.	TANAMI FM.	AKEYO FAUNA
17					
23 24					
	EOCENE-OLIGOCENE	MURO GROUP	MURO GROUP	MURO GROUP	ASAGAI- PORONAI FAUNA
30 36					

Figure 2. Stratigraphic classification of the Muro and Kumano Groups, in association with the molluscan faunal succession.

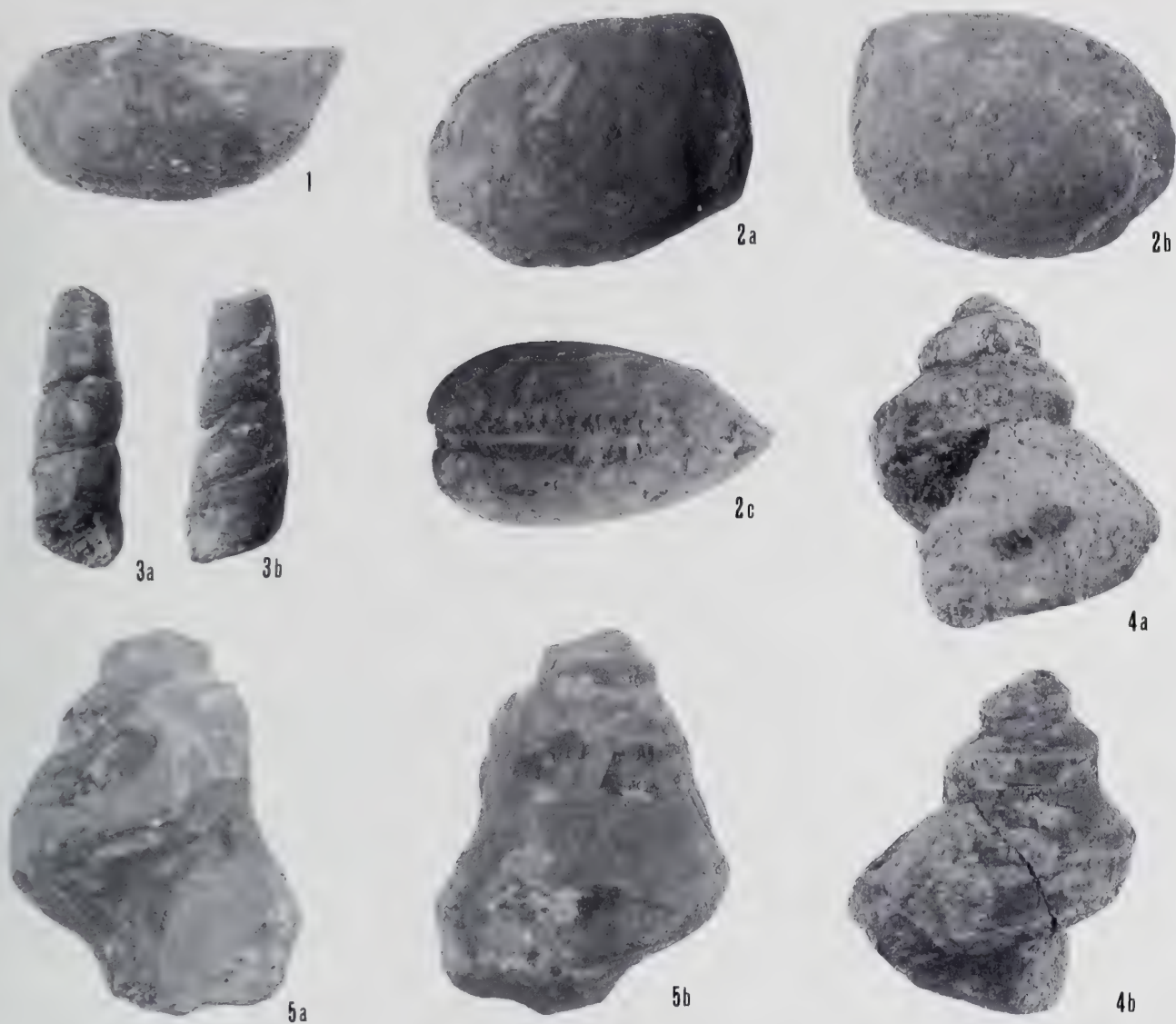
Table 1. Occurrences of fossil mollusks in the Tanami Formation. A, abundant (10 or more individuals); C, common (5 to 9 individuals); F, few (2 to 4 individuals); R, rare (one individual). One individual is defined herein as consisting of more than half of a separated valve or an articulated pair of bivalves, and more than half of a gastropod specimen.

Species	Locality		
	T1	T2	T3
Bivalvia:			
<i>Malletia poronaica</i> (Yokoyama)			R
<i>Portlandia</i> ( <i>Portlandella</i> ) <i>watasei</i> (Kanehara)	C	C	C
<i>Acila</i> ( <i>Acila</i> ) <i>kiiensis</i> Masuda et Katto			R
<i>Acila</i> sp.			R
<i>Caryocorbula</i> ? sp.			R
" <i>Teredo</i> " sp.		A	
Gastropoda:			
<i>Turritella</i> sp.		C	
<i>Trominina hokkaidoensis</i> (Hayasaka et Uozumi)	F	R	

the upper Eocene Poronai Formation in the Ishikari coalfield, central Hokkaido. The lower Oligocene Momijiyama Formation in the Ishikari coalfield has yielded several species, including *T. hokkaidoensis*, *T. onnaica* (Yokoyama), *T. ishikariensis* (Hayasaka and Matsui), *T. yubariensis* (Hayasaka and Uozumi), and *T. umbelliformis* (Hayasaka and Uozumi) (Hayasaka and Matsui, 1951; Hayasaka and Uozumi, 1954).

In addition, Honda (1989) recorded *T. japonica*, *T. hokkaidoensis*, *T. ishikariensis*, *T. umbelliformis*, and *T. dispar* (Takeda) from the lower Oligocene Ombetsu Group





**Figure 3.** 1. *Portlandia* (*Portlandella*) *watasei* (Kanehara).  $\times 1.4$ , Loc. T2, MES\* 1034. 2a-c. *Acila* (*Acila*) *kiiensis* Masuda and Katto.  $\times 1.4$ , Loc. T3, MES 1035. 3a, b. *Turritella* sp.  $\times 1.6$ , Loc. T2, MES 1036. 4, 5. *Trominina hokkaidoensis* (Hayasaka and Uozumi). 4a, b;  $\times 1.5$ , Loc. T2, MES 1037. 5a, b;  $\times 1.5$ , Loc. T1, MES 1038. \*Abbreviation for the Department of Earth Sciences, Faculty of Education, Mie University.

in the Kushiro coalfield, eastern Hokkaido. The southernmost record of *Trominina* is *T. japonica* from the upper lower Oligocene Yamaga Formation in the Ashiya Group of Kyushu, southern Japan (Tomita and Ishibashi, 1990). This suggests that *Trominina* migrated from Hokkaido and further northward to the Kii Peninsula and Kyushu, southern Japan, in accordance with the Eocene-Oligocene transition global cooling trend. In contrast to these Paleogene records, *T. bicordata* (Hatai and Koike, 1957) from the lower Miocene Hota Group in the Boso Peninsula, central Honshu, is the youngest record of *Trominina* in Japan.

Based on these records of *Trominina*, the presence of

*Trominina* in the Tanami Formation suggests that the basal part of the Tanami Formation, which also contains the Asagai-Poronai fauna, is of Oligocene rather than Miocene age. Honda *et al.* (1998) recorded the Akeyo fauna (Itoigawa, 1987; early Miocene, ca. 18 to 16 Ma; Figure 2) from the Shimosato Formation of the Ukui area in the southeastern Kii Peninsula. The basal part of the Tanami Formation contains an older fauna than does the partly coeval Shimosato Formation. The Tanami Formation as a whole is assigned to the Oligocene to early Miocene age (Figure 2).

The presence of Asagai-Poronai mollusks in the upper

part of the Muro Group first implied an Oligocene to early Miocene age for these strata (Mizuno, 1973). This is the southernmost record of the Asagai-Poronai fauna; however, it is now known to range from the late Eocene to early Oligocene in Hokkaido and northeast Honshu, northern Japan (Honda, 1994). In addition, Suzuki (1988) assigned the Aikawa Formation, in the upper part of the Muro Group, to the early to earliest middle Eocene age, based on radiolarians. Accordingly, the Shimotsuyu Formation, which is correlative with the Aikawa Formation (Tateishi *et al.*, 1979), is tentatively treated here as an Eocene to Oligocene unit (Figure 2).

### Systematic description

Family Buccinidae Rafinesque, 1815

Genus *Trominina* Oyama and Mizuno, 1958

*Type species.*—*Ancistrolepis japonicus* Takeda, 1953.

*Trominina hokkaidoensis* (Hayasaka et Uozumi, 1954)

Figure 3.4, 3.5

*Ancistrolepis yudaensis* Otuka var. *ishikariensis* Hayasaka and Matsui, 1951, p. 334, pl. 1, fig. 3 (*non* fig. 4).

*Ancistrolepis hokkaidoensis* Hayasaka and Uozumi, 1954, p. 402, pl. 25, fig. 8, pl. 26, fig. 5.

*Trominina hokkaidoensis* (Hayasaka and Uozumi). Oyama *et al.*, 1960, p. 63, pl. 10, fig. 2 (reproduced from Hayasaka and Uozumi, 1954); Kanno and Ogawa, 1964, p. 291, pl. 4, fig. 3; Honda, 1989, p. 100, pl. 10, fig. 11.

*Neptunea dispar* Takeda. Katto and Masuda, 1978, pl. 1, fig. 5.

*Material examined.*—Three specimens (MES coll. cat. nos. 1037, 1038, 1039).

*Remarks.*—This species is characterized by a high spire ornamented with one relatively weak but acutely expanded keel on the middle part of the whorl. Hayasaka and Matsui (1951, p. 334, pl. 1, figs. 3, 4) erected *Ancistrolepis yudaensis* Otuka var. *ishikariensis* from the Momijiyama Formation (lower Oligocene) of the Ishikari coalfield, central Hokkaido. Hayasaka and Uozumi (1954) later proposed *Ancistrolepis hokkaidoensis* from the Momijiyama Formation, and they doubtfully cited a specimen (Hayasaka and Matsui, 1951, pl. 1, fig. 3) as *A. hokkaidoensis*. *Trominina hokkaidoensis* differs from *T. ishikariensis* in having a weaker keel on the middle part of the whorl.

Gladenkov *et al.* (1988) synonymized *T. onnaica* (Yokoyama), *T. yubariensis*, *T. japonica*, *T. ishikariensis*, *T. hokkaidoensis*, *T. umbelliformis*, and *T. bicordata* with *T. angasiana* (Yokoyama) after studying the Eocene to Oligocene buccinids in Kamchatka. *Trominina yubariensis* and *T. umbelliformis* are characterized by a clearly ex-

panded keel on the middle part of the whorl, as is *T. angasiana*. However, *Trominina onnaica*, *T. japonica*, *T. ishikariensis*, *T. hokkaidoensis*, and *T. bicordata* all bear a relatively weak keel, which differentiates them from *T. angasiana*. Although the taxonomy of the above listed species should be further studied, they are considered here to differ from one another by the surface ornamentation and the outline of whorls.

*Trominina hokkaidoensis* most closely resembles *T. japonica*, known from the middle Eocene to upper Oligocene 'Maoka' Group in southern Sakhalin, Russia (Takeda, 1953; Kano *et al.*, 2000). However, *T. hokkaidoensis* has a more distinctly expanded body whorl than does *T. japonica*. Katto and Masuda (1978, pl. 1, fig. 5) illustrated *Neptunea dispar* from the Tanami Formation, which is assigned here to *T. hokkaidoensis* based on its more acutely elevated spire.

*Associated fauna.*—The present species is associated with such sublittoral to bathyal dwellers as *Portlandia watasei* and *Turritella* sp. (Table 1).

*Occurrence.*—Loc. T1, T2.

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# Migration and speciation of the *Loxoconcha japonica* species group (Ostracoda) in East Asia

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**Abstract.** Eighty-five fossil and Recent species of the genus *Loxoconcha* (Crustacea: Ostracoda) from East Asia are systematically reexamined. On the basis of carapace morphology, the genus *Loxoconcha* from East Asia is divided into five species groups: *L. pulchra*, *L. optima*, *L. japonica*, *L. uranouchiensis* and *L. japonica* species groups. The migration and speciation patterns of four species of the *L. japonica* species group are as follows. In Late Miocene, *L. liljeborgii* and *L. tumulosa* were distributed over the Paleo-Indian Ocean. In Early Pliocene time, these species migrated to the Western Pacific and *L. japonica* evolved from populations of *L. tumulosa* by peramorphic evolution. In the Middle Pleistocene, *L. shanhaiensis* evolved from populations of *L. japonica* in the Ryukyu Islands by paedomorphic evolution.

**Key words:** East Asia, *Loxoconcha*, Ostracoda, paedomorphic evolution, paleobiogeography, peramorphic evolution,

## Introduction

The genus *Loxoconcha* was proposed by Sars (1866) with the type species *Cythere rhomboidea* Fischer (1855), based on a Recent specimen from Lervig (= Larvik), South Norway. Since then, about 550 species belonging to this genus have been identified from around the world (Kempf, 1986). The oldest fossil record is from the Eutaw Formation (late Cretaceous) of northwest Selma, Dallas City, Alabama, North America (Crane, 1965). This genus is reported from the Paleogene of four continents: North America (Hazel *et al.*, 1980; Howe, 1963; Carreño and Cronin, 1993), Australia (Mckenzie *et al.*, 1991, 1993), Africa (Cronin and Khalifa, 1979; Ahmad *et al.*, 1991) and Europe (Keij, 1957); thus its distribution had already become worldwide. Today, it is widely distributed in littoral, sublittoral and brackish-water environments throughout the world except for the polar regions (Athersuch and Horne, 1984).

The genus *Loxoconcha* is an evolutionarily successful group, with one of the highest species diversity of all ostracod genera. Its species have adapted to various habitats, often developing morphological characters in adapting to microhabitats.

In East Asia, 85 species of *Loxoconcha* have been described since 1868 when Brady reported two Recent species from Batavia, Java, present-day Indonesia (Brady,

1868). Based on carapace outlines, surface ornamentation patterns, hinge structures and muscle scar patterns, *Loxoconcha* can be classified into five species groups (Figure 1). Morphological similarity among *Loxoconcha* species is affected either by the genotype or environmental interactions or both. It is possible to estimate the relative importance of each by investigating intraspecific morphological variants and their geographical, stratigraphical and ontogenetical variability. In this study, we focus on the neritic *L. japonica* species group. We compare morphological characters among species and evaluate the presumed phylogenetic relationships among species based on inter-specific morphological similarities. Finally, we consider geographic dispersal processes and mechanisms of adaptation to local environments.

## Material

This study is based mainly on Recent and fossil faunal slides housed at Shizuoka University. Collections of *Loxoconcha* come from 35 localities (23 Recent; 12 fossil) which range geographically from Suttu Bay (Hokkaido, Japan) to Taiwan (Figure 2 and Table 1). All figured specimens have been deposited at the Shizuoka University Museum, Japan (SUM-CO-Number).

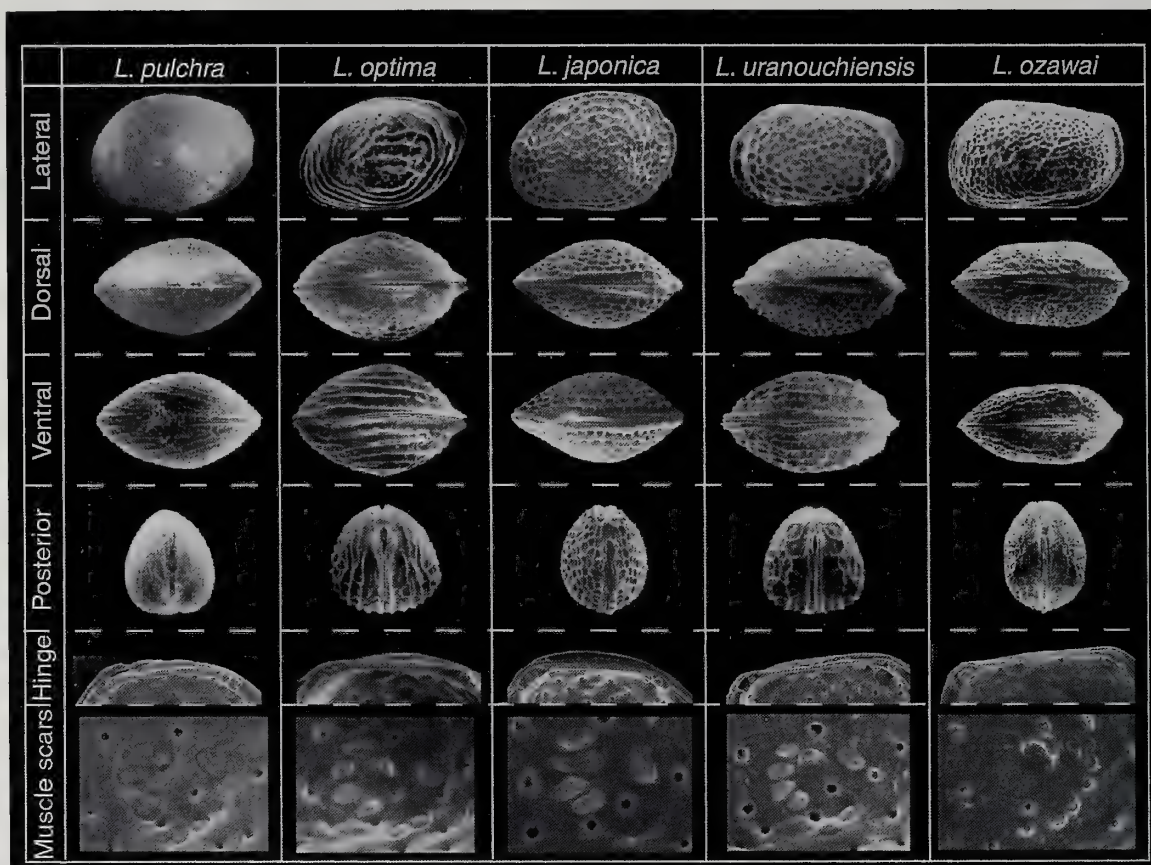


Figure 1. Five species groups of *Loxoconcha* in the East Asia, defined on the basis of their carapace morphology. Not to scale.

### Morphological classifications of genus *Loxoconcha* from East Asia

*Loxoconcha*, which includes 85 species from the East Asia, is divided into the following five species groups on the basis of carapace morphology (Figure 1). They include those species which have not been given species names (indicated by *L. sp.*) and those referred to in quotes in the literature.

*Loxoconcha pulchra* species group. — Carapace subrhomboidal in lateral view. Surface ornamentation of the carapace consists of concentrically-arranged pits or weak reticulation, except for the dorsal area. In dorsal view, ornamentation not developed. In ventral view, five pairs of ridges diverge toward anterior. Posterior element of hingement is ball-shaped. Prominent fulcral point. A total of six species are included: *L. pulchra*, *L. subcirculata*, *L. subpulchra*, *L. sp.* (Hou *et al.*, 1982), *L. sp. C* (Ikeya *et al.*, 1985), "*L. pulchra*" (in Gou *et al.*, 1981).

*Loxoconcha optima* species group. — Carapace subrhomboidal in lateral view. Surface ornament of the carapace consists of concentrically-arranged ridges or pits as located

around the position of the muscle scar, except for the dorsal area. In dorsal view, ornamentation not developed. In ventral view, five pairs of ridges run parallel from anterior to posterior. Posterior element of hingement is composed of three teeth. Prominent fulcral point. A total of sixteen species are included: *L. chinzeii*, *L. hemicrenulata*, *L. ikeyai*, *L. medioconvexa*, *L. optima*, *L. orientarica*, *L. pleistocenica*, *L. taiwanensis*, *L. tamakazura*, *L. tarda*, *L. sp.* (Hu, 1978), *L. sp.* (Ishizaki, 1984), *L. sp.* (Yajima, 1988), "*L. pulchra*" (in Yajima, 1988), "*L. sinensis*" (in Gou *et al.*, 1981), "*L. sinensis*" (in Zhao *et al.*, 1985).

*Loxoconcha japonica* species group. — Carapace subrhomboidal in lateral view. Surface ornament of the carapace consists of concentrically-arranged pits or coarse reticulation centered around the muscle scars. In dorsal view, a pair of ridges converges toward the anterior. In ventral view, five pairs of ridges developed that run parallel from anterior to posterior. Posterior element of hingement is ball-shaped. Fulcral point not prominent. The following four species are included: *L. japonica*, *L. lilljeborgii*, *L. shanghaiensis*, *L. tumulosa*.

*Loxoconcha uranouchiensis* species group. — Carapace



**Table 1.** Sample localities for *L. japonica* species group from East Asia. Sample numbers corresponds to those in Figure 2. Abbreviations: Alg. = Algae; M. = Mud; St. = Silt; Sd = Sand; R. = Rock; f. = fine; m. = medium; c. = coarse; mdy. = muddy; sdy. = sandy; gry. = gravelly; L. = late; M. = middle; E. = early; Ls. = Limestone; Pref. = Prefecture; Penin. = Peninsula; Is. = Island; Ja = *L. japonica*; Sh = *L. shanghaiensis*; Tu = *L. tumulosa*; Li = *L. lilljeborgii*.

Recent materials						
Sample number	Localities	Latitude (N)	Longitude (E)	Depth (m)	Remarks	Species
1a	Suttu Bay	42°48.9'	140°18.0'	22	R.	Ja
1b	"	42°47.8'	140°16.2'	34	f.-Sd.	Ja
1c	"	42°47.2'	140°18.7'	9	R.	Ja
1d	"	42°47.2'	140°15.6'	26	f.-Sd.	Ja
1e	"	42°46.7'	140°17.9'	11	f.-Sd.	Ja
1f	"	42°46.7'	140°15.6'	17	f.-Sd.	Ja
1g	"	42°46.2'	140°16.5'	7	c.-Sd.	Ja
1h	"	42°46.2'	140°15.0'	5	c.-Sd.	Ja
2	Otsuchi Bay	39°19.6'	141°55.0'	15	c.-Sd.	Ja
3	Imagawa	38°24.6'	139°28.1'	0	Alg.	Ja
4	Aikawa	38°02.4'	138°14.3'	0	Alg.	Ja
5	Hayase	35°37.0'	135°54.7'	1	Alg.	Ja
6	Kagoshima	35°39.5'	134°46.8'	0	Alg.	Ja
7	Off Shimane	36°13.9'	133°06.0'	96	mdy., f.-m.-Sd.	Ja
8	Misaki	35°09.5'	139°37.0'	0	Sea glass	Ja
9	Osezaki	35°06.3'	138°47.4'	1	Alg.	Ja
10	Ago Bay	34°57.1'	136°40.5'	7	f.-Sd.	Ja
11	Hanesaki	33°22.0'	134°02.4'	0	Alg.	Ja
12	Uwajima Bay	33°10.8'	132°29.9'	5	v. c.-Sd.	Ja
13	Tsuyasaki	33°47.4'	130°27.7'	2	m.-Sd.	Ja
14	Danjyo Islands	32°01.9'	128°23.1'	86	f.-Sd.	Ja
15	Okawa-minato	31°14.6'	130°24.8'	0	Alg.	Ja
16	Tanega-shima Is.	30°10.3'	130°52.7'	96	c. shelly-Sd.	Ja
17	Amami-o-shima Is.	28°07.5'	129°22.0'	4	coral Sd.	Ja, Sh
18	Tokuno-shima Is.	27°51.6'	128°57.7'	0	Alg.	Ja, Tu
19	Yoron Is.	27°02.9'	128°27.3'	0	Alg.	Ja, Sh, Tu, Li
20a	Nago Bay	26°34.1'	127°56.4'	38	m.-St.	Sh
20b	"	26°39.3'	127°51.5'	59	m.-Sd.	Ja, Sh
20c	"	26°37.7'	127°52.2'	22	m.-Sd.	Ja, Sh
20d	"	26°36.1'	127°53.5'	40	c.-Sd.	Ja, Sh
20e	Nakagusuku Bay	27°19.2'	127°52.0'	4	sdly.-M.	Ja, Li
20f	"	26°16.8'	127°50.3'	6	gry.-Sd.	Sh, Li
20g	"	26°15.9'	127°54.3'	21	Sd.	Ja, Sh, Tu, Li
20h	"	26°15.3'	127°53.1'	4	gry.-Sd.	Ja, Sh
20i	"	26°15.0'	127°52.3'	20	Sd.	Ja, Sh
20j	"	26°12.8'	127°55.0'	48	Sd.,-M.	Ja, Sh, Li
20k	"	26°12.5'	127°52.9'	28	mdy.-Sd.	Ja, Sh, Li
20l	"	26°10.1'	127°52.8'	22	Sd.	Ja, Sh
20m	"	26°07.8'	127°53.9'	70	gry.-Sd.	Ja, Sh, Li
21	Off Miyako Is.	24°47.9'	127°37.4'	124	c.-Sd.	Sh
22	Sekisei-sho	24°27.4'	124°03.3'	167	f.-Sd.	Ja, Sh
23	Hengchun Penin.	21°56.0'	120°49.0'	0	Alg.	Sh, Tu
Fossil materials						
Sample number	Formation (age)	Localities	Latitude (N)	Longitude (E)	Remarks	Species
a	Hamada (L. Pleistocene)	Shimokita Penin.	41°10.3'	141°16.4'		Ja
b1	Sawane (Pliocene)	Sado Is.	37°59.6'	138°15.6'		Ja
b2	Sawane (Pliocene)	"	37°59.3'	138°15.9'		Ja
c1	Hiradoko (L. Pleistocene)	Noto Penin.	37°27.0'	137°18.2'		Ja
c2	Miyainu (L. Pleistocene)	"	37°20.2'	137°13.8'		Ja
c3	Numashiro (L. Pleistocene)	"	35°19.4'	139°15.4'		Ja
d1	Ninomiya (L. Pleistocene)	Oiso Hill	35°18.9'	139°15.1'		Ja
d2	"	"	35°18.4'	139°15.4'		Ja
d3	"	"	35°18.2'	139°15.7'		Ja
e	Takahama (Holocene)	Fukui Pref.	35°29.2'	135°33.3'		Ja
f	Hamamatsu (Holocene)	Hamana-ko	34°44.8'	137°36.5'		Ja
g	Ananai (Plio-Pleistocene)	Shikoku	33°29.4'	133°56.7'		Ja
h	Shimo-jiro (M. Pleistocene)	Okino-erabu Is.	27°24.5'	128°38.3'		Sh
i	Maja (E. Pliocene)	Kume Is.	26°22.6'	126°47.4'		Ja
j1	Yonabaru (L. Pliocene)	Okinawa Is.	26°09.7'	127°46.7'		Ja
j2	Chinen Sand (E. Pleistocene)	Okinawa Is.	26°07.3'	127°43.8'		Ja
k	Tungshiao (L. Pleistocene)	Taiwan	24°36.0'	120°43.0'		Sh
l1	Hengchun Ls. (L. Pleistocene)	Taiwan	21°59.0'	120°43.0'		Ja, Sh, Li
l2	Hengchun Ls. (L. Pleistocene)	Taiwan	21°55.0'	120°51.0'		Sh, Tu

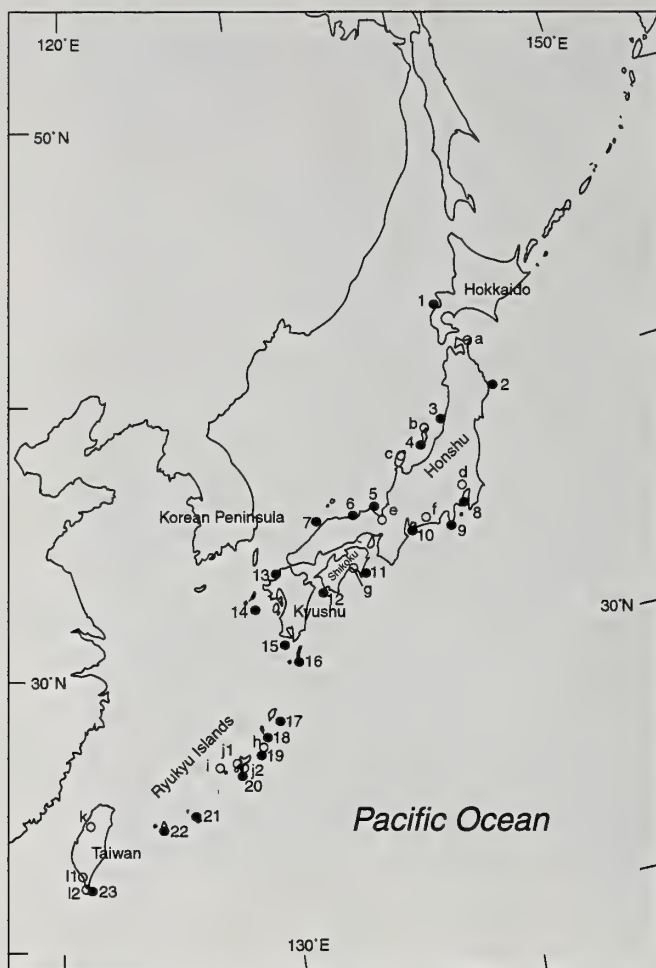


Figure 2. Map showing sampling localities. Numbers and lower case letters correspond to the sample numbers in Table 1.

subrhomboidal to oblong in lateral view. Surface ornament of the carapace consists of reticulation. In dorsal view, the carapace is covered with irregular reticulation. In ventral view, three- or four-pairs of ridges run parallel from anterior to posterior, the most ventral pair being developed only in the anterior region. Posterior element of hingement is ball-shaped. Prominent fulcral point. A total of forty-three species are included: *L. bispinosa*, *L. bizenensis*, *L. brevia*, *L. crassella*, *L. crispatum*, *L. epeterseni*, *L. hanachirusato*, *L. harimensis*, *L. hattorii*, *L. kattoi*, *L. kitanipponica*, *L. malayensis*, *L. nozokiensis*, *L. paiki*, *L. pashihaiensis*, *L. prolaeta*, *L. sinensis*, *L. tata*, *L. tosaensis*, *L. tosamodesta*, *L. triconicula*, *L. uranouchiensis*, *L. ventispina*, *L. viva*, *L. xuwenensis*, *L. yinggehaiensis*, *L. zamia*, *L. zhejiangensis*, *L. sp. A* (Huh, 1992), *L. sp. B* (Ishizaki, 1968), *L. sp. B* (Lee, 1990), *L. sp. C* (Huh, 1992), *L. sp. 2* (Yamane, 1998), "*L. hattorii*" (in Cai, 1982), "*L. hattorii*" (in Wang and Zhang, 1987), "*L. kattoi*" (in Ruan and Hao, 1988), "*L. sinensis*" (in Gou et al., 1981), "*L.*

*sinensis*" (in Ruan and Hao, 1988), "*L. uranouchiensis*" (in Cai and Chen, 1987), "*L. cf. uranouchiensis*" (in Gou et al., 1983), "*L. uranouchiensis*" (in Tabuki et al., 1987), "*L. uranouchiensis*" (in Yamane, 1998), "*L. viva*" (in Wang et al., 1988).

*Loxoconcha ozawai species group*.—Carapace subrhomboidal to oblong in lateral view. Surface ornamentation of the carapace consists of weak reticulation. In dorsal view, the carapace is covered with weak, irregular reticulation. In ventral view, two pairs of weak ridges converge toward anterior. Posterior element of hingement is ball-shaped. Prominent fulcral point. The following sixteen species are included: *L. binhaiensis*, *L. elliptica*, *L. fujianensis*, *L. gigantea*, *L. hataii*, *L. ocellata*, *L. ozawai*, *L. subkotoriforma*, *L. sp.* (Ikeya et al., 1992), *L. sp.* (Tsukagoshi and Kamiya, 1996), *L. sp. B* (Huh, 1992), *L. sp. B* (Ishizaki, 1971), *L. sp. D* (Huh, 1992), *L. sp. 1* (Ozawa, 1996), *L. sp. 1* (Yamane, 1998), "*L. sinensis*" (in Zhao and Wang, 1988).

### Natural history of *Loxoconcha japonica* species group

#### Morphological characters

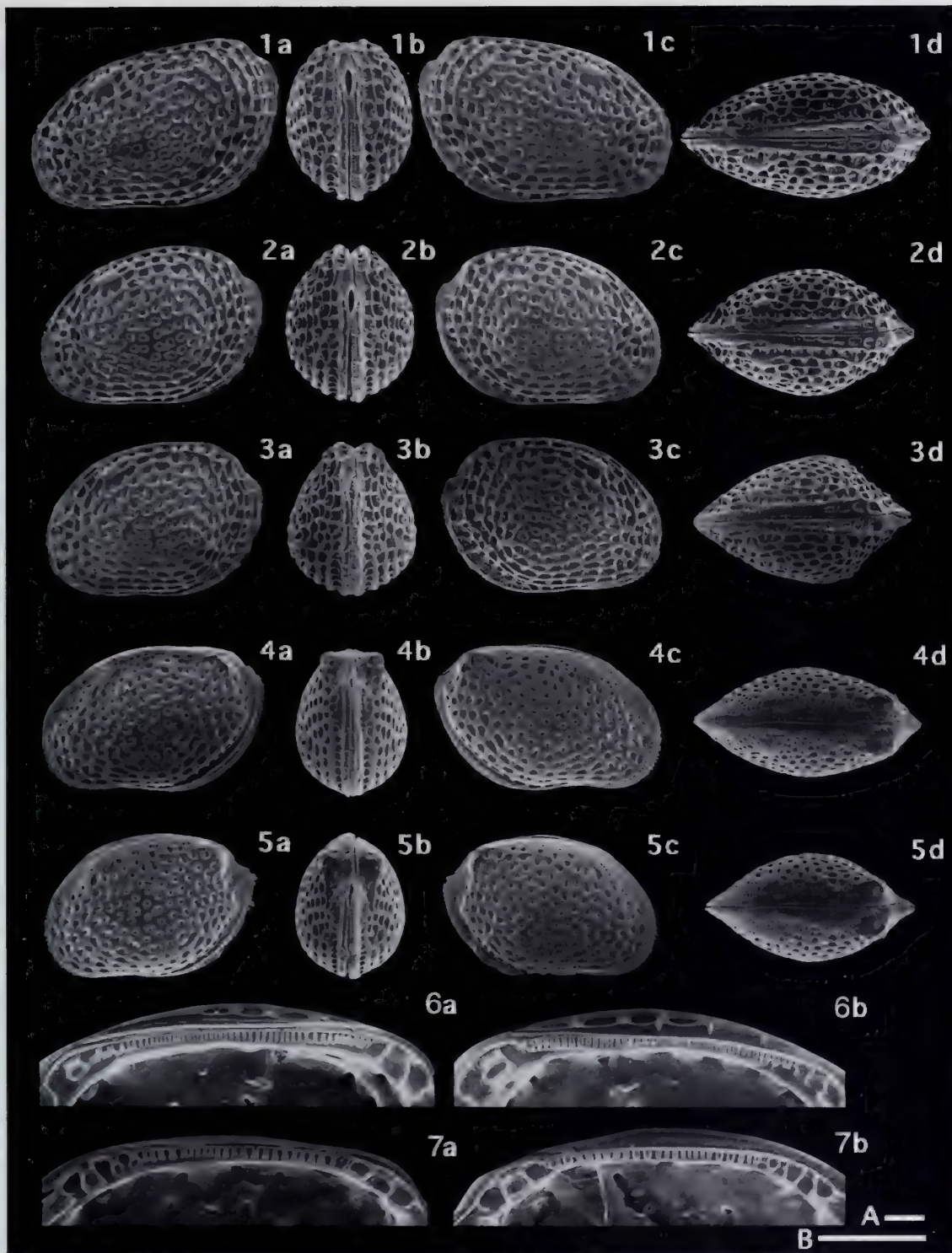
In order to characterize the *L. japonica* species group, four species of the group were compared in terms of carapace morphology (Figures 3, 4), pore system (Figure 5), appendages (Figure 6) and male copulatory organ (Figure 7). The following summarizes the morphology of this species group.

*Carapace outline*.—Carapace subrhomboidal in lateral view. Dorsal margin straight and sloped toward anterior or arched dorsally; anterior margin with an oblique curvature; ventral margin slightly concave at mid-anterior area; posterior margin curved toward the dorsal. Caudal process protrudes prominently toward posterodorsal. In dorsal and ventral view, carapace diamond- to wedge-shaped. In posterior view, carapace elliptical to egg-shaped. Large sexual dimorphism; in lateral view, male more elongate.

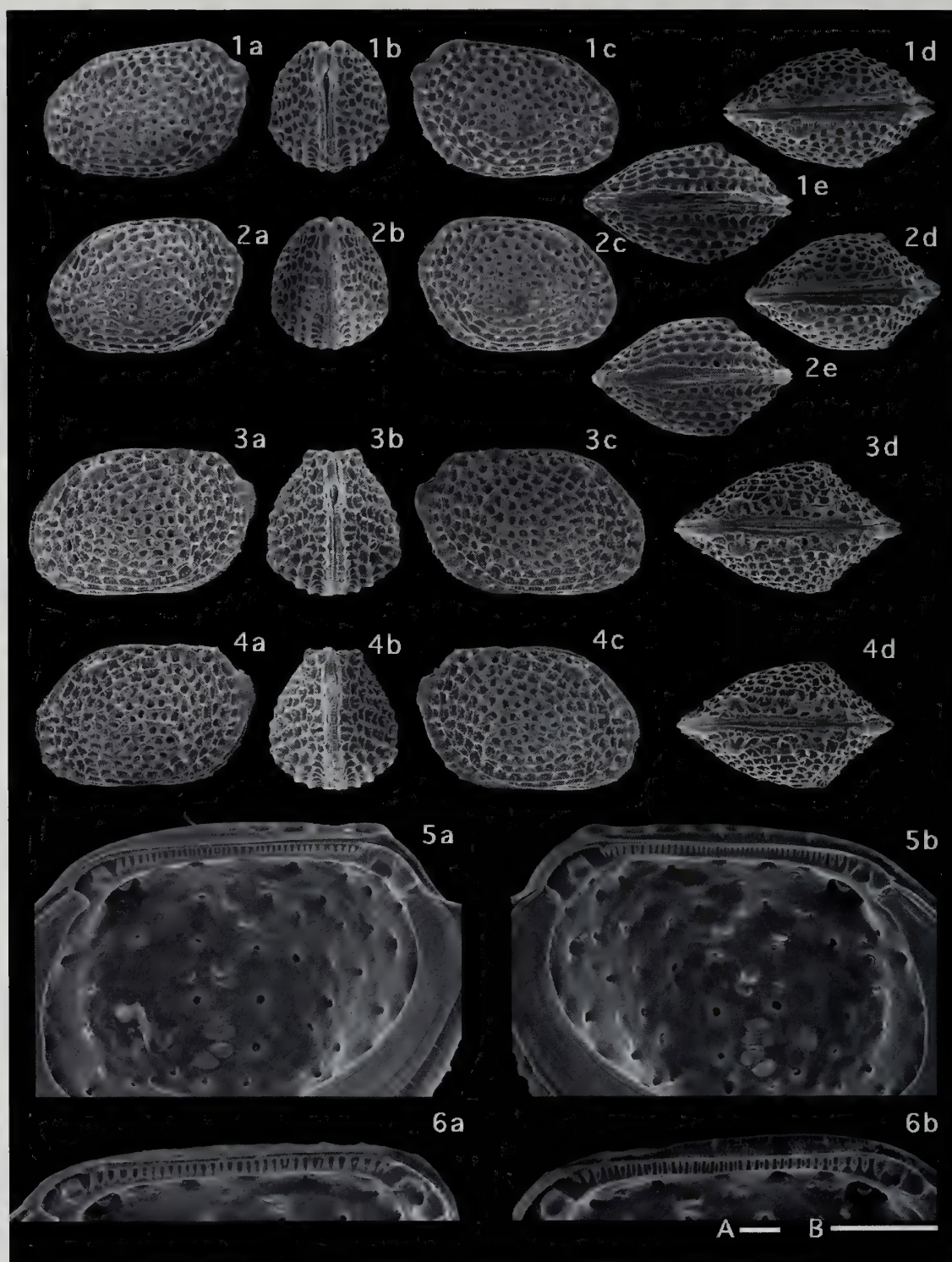
*Carapace ornamentation*.—Surface of the carapace is entirely ornamented with pits or coarse reticulation in lateral view. The ornamentation is concentrically arranged, consisting of eight rings centered around the position of the muscle scar. Posteroventral alate ridge and/or postero-dorsal protuberance are/is sometimes developed. In ventral view, five pairs of ridges run parallel from the anterior to posterior margins. In dorsal view, a pair of ridges converges toward the anterior. In posterior view, on the ventral side of the posterior margin, four pairs of short ridges are developed that consist of reticulations arranged parallel to the posterior margin. On the dorsal side of the posterior margin, on the other hand, radially-developed ridges centered near the position of the caudal process intersect ridges that parallel the posterior margin.

*Hinge*.—Gongylodont. In left valve, anterior element is



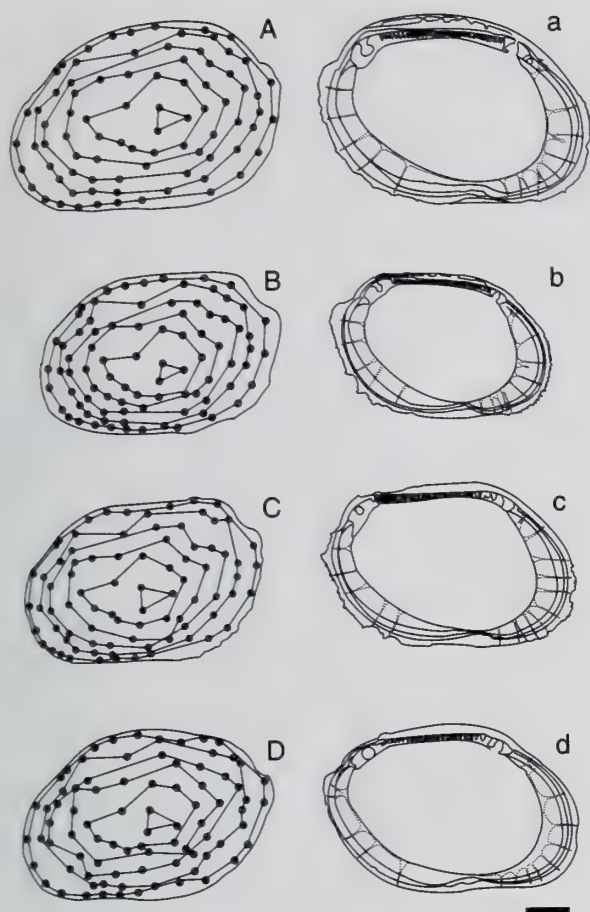


**Figure 3.** 1-3, 6. *Loxoconcha japonica* Ishizaki, 1968. 4, 5, 7. *Loxoconcha lilljeborgii* Brady, 1868. 1. A male carapace of the same specimen in external left lateral view (a), posterior view (b), right lateral view (c) and dorsal view (d) from sample no. 8 (SUM-CO-1269). 2. A female carapace of the same specimen in external view (a-d) from sample no. 8 (SUM-CO-1270). 3. A female carapace of the same specimen with alate ridge at the posteroventral area in external view (a-d) from sample no. 17 (SUM-CO-1271). 4. A male carapace of the same specimen in external view (a-d) from sample no. 19 (SUM-CO-1305). 5. A female carapace of the same specimen in external view (a-d) from sample no. 19 (SUM-CO-1306). 6. Hingement of female right (a) (SUM-CO-1272) and left (b) (SUM-CO-1273) valves from sample no. 19. 7. Hingement of female right (a) (SUM-CO-1307) and left (b) (SUM-CO-1308) valves from sample no. 19. Scale bars = 100  $\mu$ m (A for 1-5; B for 6, 7).



**Figure 4.** 1, 2, 5. *Loxoconcha shanghaiensis* Hu, 1981. 3, 4, 6. *Loxoconcha tumulosa* (Hu, 1979). 1. A male carapace of the same specimen in external left lateral view (a), posterior view (b), right lateral view (c), dorsal view (d) and ventral view (e) from sample no. 17 (SUM-CO-1284). 2. A female carapace of the same specimen in external view (a-e) from sample no. 17 (SUM-CO-1285). 3. A male carapace of the same specimen in external view (a-d) from sample no. 23 (SUM-CO-1294). 4. A female carapace of the same specimen in external view (a-d) from sample no. 23 (SUM-CO-1295). 5. Hingement and muscle scars of female right (a) (SUM-CO-1286) and left (b) (SUM-CO-1287) valves from sample no. 20h. 6. Hingement of female right (a) (SUM-CO-1296) and left (b) (SUM-CO-1297) valves from sample no. 23. Scale bars = 100  $\mu$ m (A for 1-4; B for 5, 6).





a down-turned claw, median element with 25–51 teeth, and posterior element is ball-shaped.

**Ocular sinus.**—In all four species, nipple-like projection develops at the dorsoposterior portion in internal view.

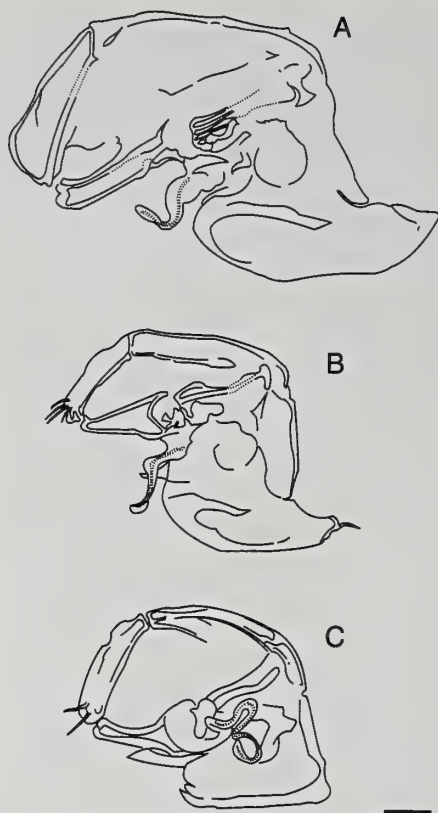
**Muscle scars.**—Four adductor muscle scars in an arcuate row, concave anterior. The upper of the two middle ones is larger than the rest. A bean-shaped frontal scar of occurs in front of the lower two adductor muscle scars. Two mandibular scars in front and below the lowest adductor muscle scar. Fulcral point absent.

**Pore system.**—In all species, 83 sieve-type pores are distributed in each adult valve, and each pore opening location resembles among four species (left side of Figure 5). Distribution of radial pores falls into two patterns (right side of Figure 5), depending on numbers of pores extending to marginal area: a), 11 in anterior area and 5 in posterior area: *L. japonica*, *L. shanghaiensis* and *L. tumulosa*; b), 10 and 5, respectively: *L. lilljeborgii*. Moreover, *L. lilljeborgii* is differentiated from the other three species, in that

**Figure 5.** The pattern of distribution pores in external view (A–D) and the radiation of radial pores in internal view (a–d) on four species of the *Loxoconcha japonica* species group (all specimens are female left valves). **A, a.** *Loxoconcha japonica* Ishizaki, 1968 (A, SUM-CO-1262; a, SUM-CO-1263). **B, b.** *Loxoconcha shanghaiensis* Hu, 1981 (B, SUM-CO-1274; b, SUM-CO-1275). **C, c.** *Loxoconcha tumulosa* (Hu, 1979) (C, SUM-CO-1288; c, SUM-CO-1289). **D, d.** *Loxoconcha lilljeborgii* Brady, 1868 (D, SUM-CO-1298; d, SUM-CO-1299). Scale bar = 100  $\mu$ m.



**Figure 6.** Chitinous parts of *Loxoconcha shanghaiensis* Hu, 1981 from sample no. 20f. **A,** antennule; **B,** antenna (SUM-CO-1277); **C,** mandible; **D,** maxilla (SUM-CO-1278); **E,** first thoracic leg; **F,** second thoracic leg; **G,** third thoracic leg (SUM-CO-1279). Scale bar = 50  $\mu$ m.



**Figure 7.** Male copulatory organs of three species of *Loxoconcha japonica* species group. **A.** *Loxoconcha japonica* Ishizaki, 1968 from sample no. 8 (SUM-CO-1264). **B.** *Loxoconcha shanhaiensis* Hu, 1981 from sample no. 20f (SUM-CO-1276). **C.** *Loxoconcha lilljeborgii* Brady, 1868 from sample no. 19 (SUM-CO-1300). Scale bar = 50  $\mu$ m.

the upper two pores of at the posterior margin branch in the middle of the marginal infoldment.

**Appendages.**—No significant differences are observed among the four species.

**Male copulatory organ.**—Except for *L. tumulosa*, outline of the basal capsule is trapezoidal and costa are developed in three species. In detail, however, several differences are observed among the three species in morphology of the copulatory organ. Distal corner rounded in *L. lilljeborgii* but tapered in *L. japonica* and *L. shanhaiensis*; ductus ejaculatorius curved in *L. lilljeborgii* but shoehorn-shaped in *L. japonica* and *L. shanhaiensis*; clasping apparatus absent in *L. japonica*, triangular in *L. shanhaiensis* and square in *L. lilljeborgii*.

#### Ontogenetic differentiation in carapace morphology

For the carapace morphologies of the four species, the ontogenetic differentiation from the A-2 instar to the adult were compared.

**Carapace outline** (Figure 8).—The position of the maximum height shifts toward the posterior from the A-2 instar to the adult. The time of shift is at the A-1 instar for *L. japonica* and *L. lilljeborgii* and at the adult for *L. shanhaiensis* and *L. tumulosa*.

The position of the maximum width is stationary from the A-2 instar to the adult (*L. shanhaiensis* and *L. tumulosa*) or shifts to the anterior at the adult (*L. lilljeborgii* and the male of *L. japonica*).

**Carapace ornamentation** (Figure 8).—The concentric arrangement of reticulation or pits is fixed from the A-2 instar to the adult. From the A-2 instar to the adult, the developmental state of reticulation or pits, however, differs from species to species. Namely, *L. japonica* already has adult-like coarse reticulation in the A-2 instar, but *L. shanhaiensis* and *L. tumulosa* only attain coarse reticulation in the A-1 instar. *L. lilljeborgii* has pits in the A-2 and A-1 instars, and is smoothly reticulate in the adult.

The posteroventral alate ridge is well developed in the A-2 and A-1 instars of all four species. In the adult, this character is retained in *L. shanhaiensis* and *L. tumulosa*, but disappears in *L. lilljeborgii* and the male of *L. japonica*. In the female of *L. japonica*, however, some specimens keep and others lose this character.

The posterodorsal protuberance does not appear during ontogenetic development in *L. japonica* and *L. shanhaiensis*, whereas, it appears from the A-1 instar onward in *L. tumulosa* and *L. lilljeborgii*.

**Hinge** (Figure 9).—Although development of the anterior element of the hinge is weak in the A-2 instar, these species clearly possess a gongylodont hinge after the A-1 instar. The number of teeth in the median element could not be counted in the A-2 instar, since it is smooth, however, from the A-1 instar onward the number of teeth is: 42–51 in *L. japonica*, 39–40 in *L. shanhaiensis*, 31–40 in *L. tumulosa*, and 25–31 in *L. lilljeborgii*.

**Ocular sinus** (Figure 9).—The nipple-like projection in the dorsoposterior area on the internal side appears after the A-2 instar for *L. japonica*, *L. shanhaiensis* and *L. tumulosa* and after the A-1 instar for *L. lilljeborgii*.

**Muscle scars** (Figure 4).—After the A-2 instar, the four species have four adductor muscle scars in an arcuate row; with no morphological variation in this feature among the species.

**Pore system** (Figure 8).—The total number of sieve-type pores per valve is the same in all four species: 54 in the A-2 instar, 73 in the A-1 instar and 83 in the adult.

From the carapace characters described above, it is thought that *L. japonica*, *L. lilljeborgii* and an ancestor of *L. shanhaiensis*–*L. tumulosa* differentiated at the A-2 instar, and that *L. shanhaiensis* and *L. tumulosa* differentiated in the A-1 instar (Figure 10).





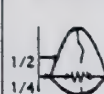
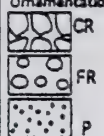



Carapace outline				Carapace ornamentation			Pore system	
Lateral Max. height AC 1/2 1/5 	Dorsal Max. width 1/2 1/3 	Posterior Max. width 1/2 1/4 	Ornamentation CR FR P 	Alate ridge 	Protuberance PT 	Numbers/valve 		
A-2	AC	1/3	1/4	CR	AR	Non	54	<i>L. japonica</i>
	AC	1/3	1/4	P	AR	Non	54	<i>L. shanhaiensis</i>
	AC	1/3	1/4	P	AR	Non	54	<i>L. tumulosa</i>
	AC	1/3	1/4	P	AR	Non	54	<i>L. lillieborgii</i>
A-1	1/2	1/3	1/4	CR	AR	Non	73	<i>L. japonica</i>
	AC	1/3	1/4	CR	AR	Non	73	<i>L. shanhaiensis</i>
	AC	1/3	1/4	CR	AR	PT	73	<i>L. tumulosa</i>
	1/2	1/3	1/4	P	AR	PT	73	<i>L. lillieborgii</i>
Adult ♀	1/2	1/3~1/2	1/4~1/2	CR	AR or Non	Non	83	<i>L. japonica</i>
	1/3	1/3	1/4	CR	AR	Non	83	<i>L. shanhaiensis</i>
	1/2	1/3	1/4	CR	AR	PT	83	<i>L. tumulosa</i>
	1/2	1/2	1/2	FR	Non	PT	83	<i>L. lillieborgii</i>
Adult ♂	1/5	1/2	1/2	CR	Non	Non	83	<i>L. japonica</i>
	1/5	1/3	1/4	CR	AR	Non	83	<i>L. shanhaiensis</i>
	1/2	1/3	1/4	CR	AR	PT	83	<i>L. tumulosa</i>
	1/5	1/2	1/2	FR	Non	PT	83	<i>L. lillieborgii</i>

Figure 8. Schematic diagram of ontogenetic differentiation of carapace morphology. Abbreviations: AC = anterior cardinal angle, H = maximum height, W = maximum width on dorsal view, W' = maximum width on posterior view, CR = coarse reticulation, FR = fine reticulation, P = pit, AR = alate ridge, PT = protuberance.

### Paleobiogeography

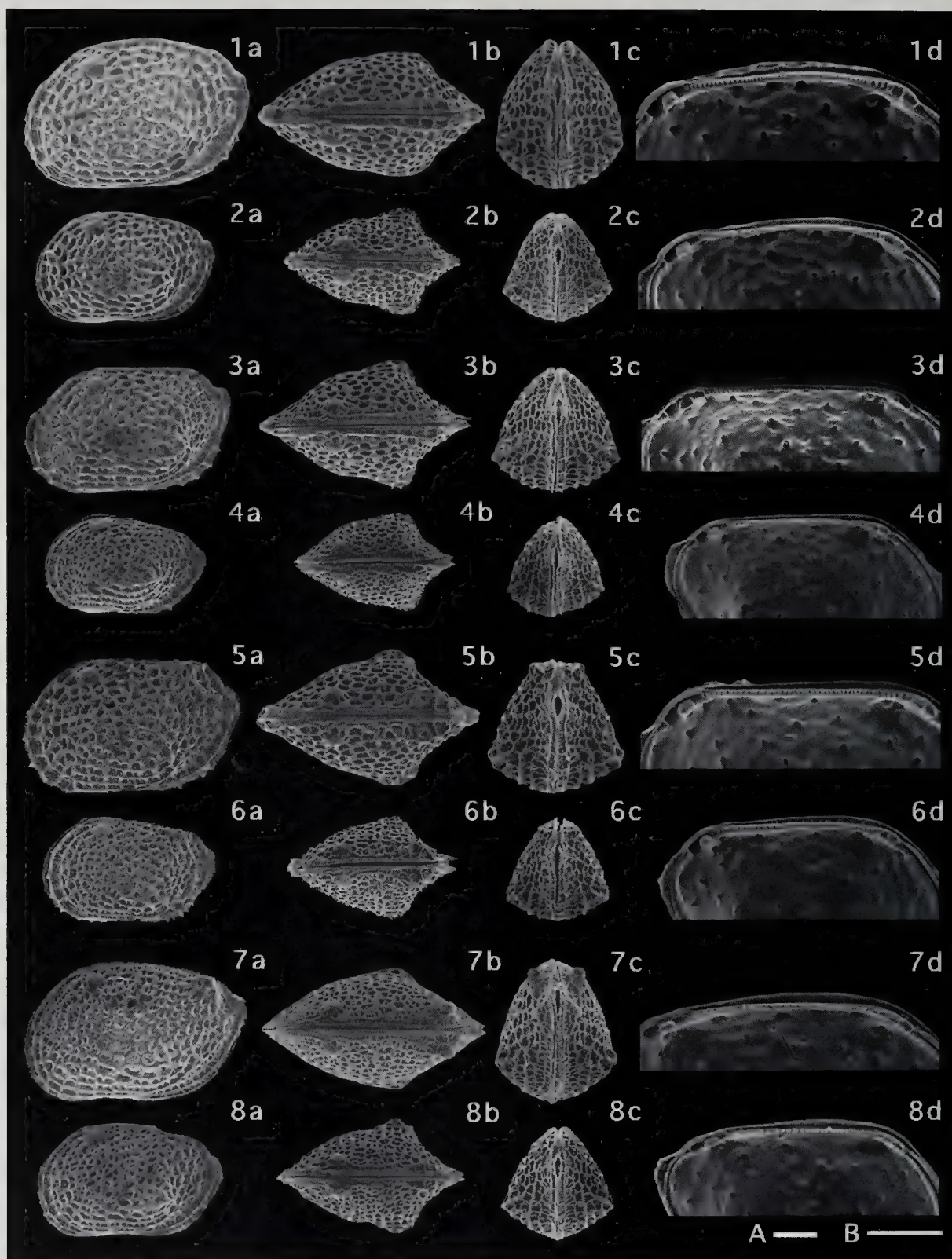
On the basis of our materials and published reports, we considered the paleobiogeographic distributions of the four species.

**Fossil distribution** (Figure 11).—The oldest specimens of *L. lillieborgii* and *L. tumulosa* occur in the Late Miocene Round Chalk and Silt Formation from the Andaman Islands of the Indian Ocean (Loc. A: Guha, 1968). Two species are also reported from the Pliocene Guiter Formation from the same region (Loc. A': Guha, 1968). These two species, however, occur also in the Late Pleistocene in the West Pacific region. Namely, *L. lillieborgii* occurs from the Late Pleistocene Hengchun Limestone from Taiwan

(Loc. E: Figure 2, 11) and in the Late Pleistocene Gundurimba Clay from Australia (Loc. C: McKenzie and Pickett, 1984), and *L. tumulosa* occurs from the Late Pleistocene Hengchun Limestone from Taiwan (Loc. D: Figure 2, loc. 12).

The oldest specimen of *L. japonica* comes from the Early Pliocene Maja Formation from Kume Island of the Ryukyus (Loc. G: Figure 2, loc. i). This species also occurs in thirteen post-Pliocene formations ranging from Taiwan to the northern part of Honshu (Locs. D, H and J-S) and in Holocene sediments from Hong Kong (Loc. B: Cao, 1998).

The oldest fossil occurrence of *L. shanhaiensis* is known





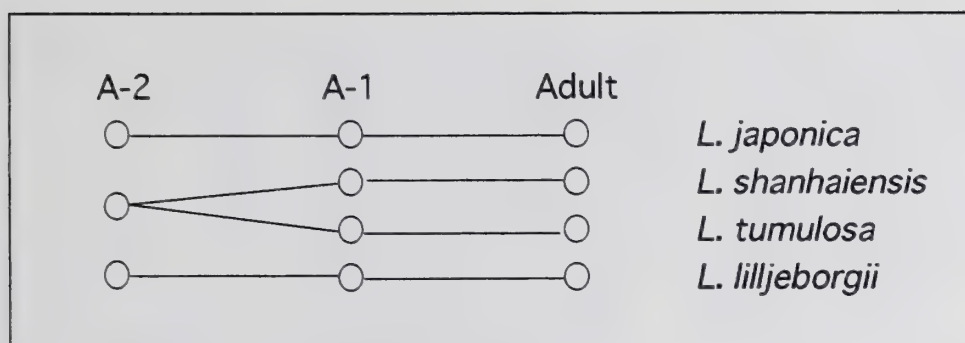


Figure 10. Ontogenetic differentiation of four species based on carapace characters.

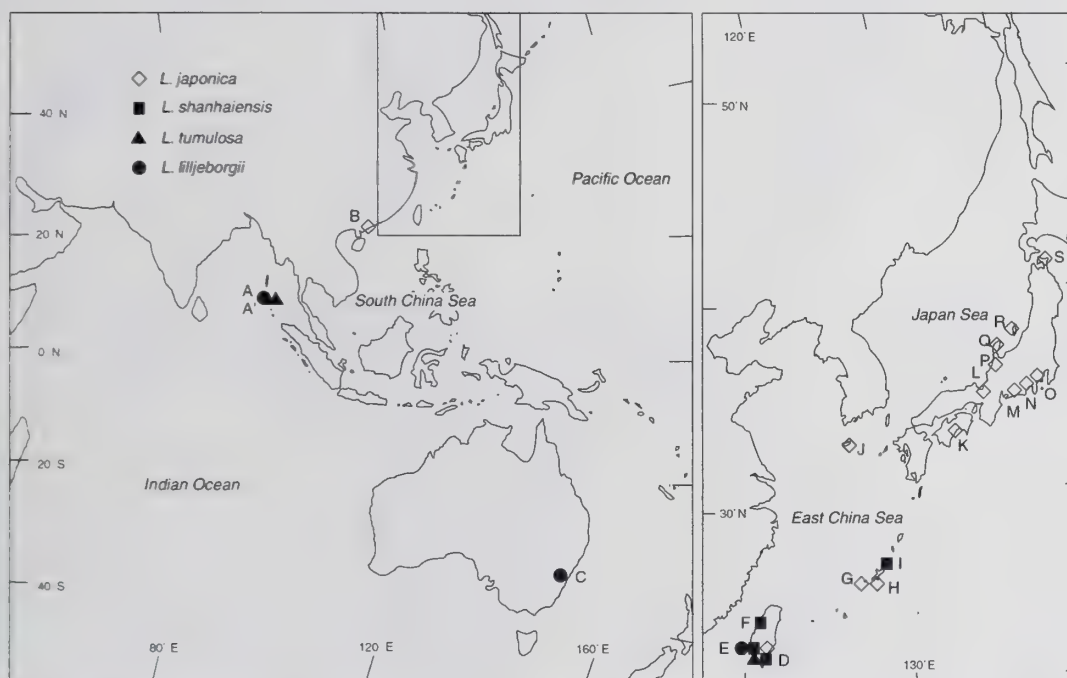
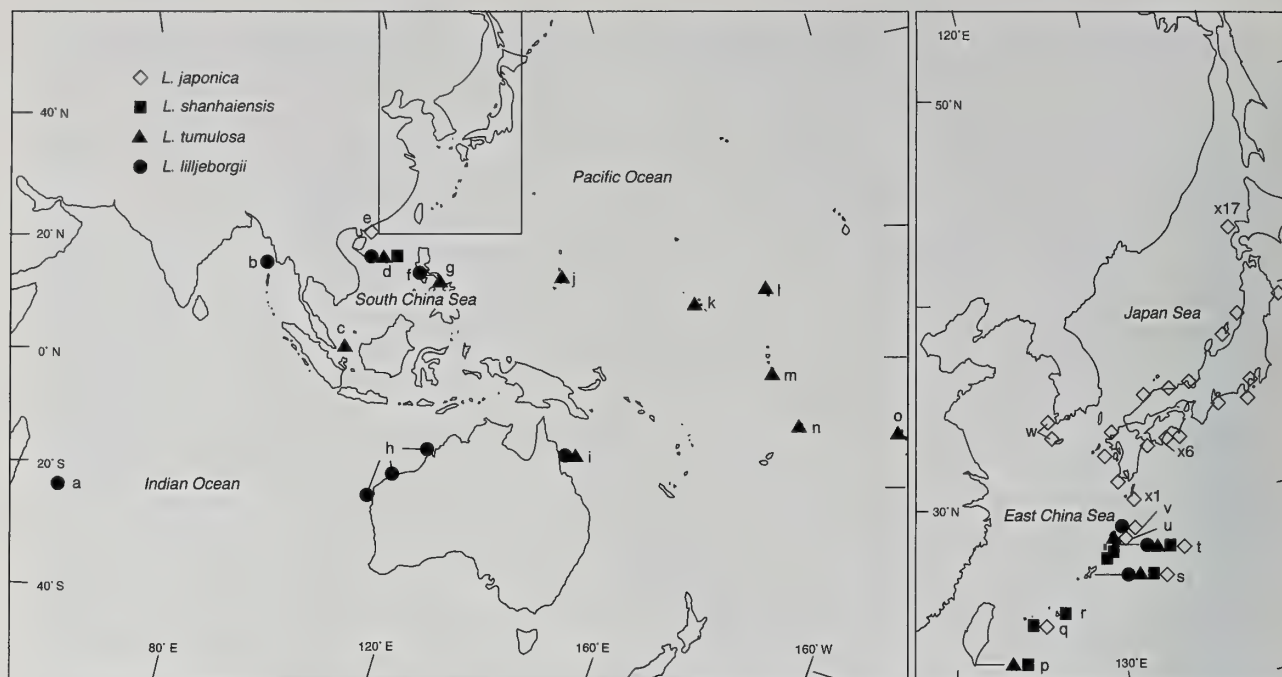


Figure 11. Geographic distribution of four species of *Loxoconcha japonica* species group (fossil). A and A' (Late Miocene Round Chalk and Silt Formation and Pliocene Guiter Formation; Guha, 1968); B (Holocene Hang Hau Formation; Cao, 1998); C (Late Pleistocene Gundurimba Clay; McKenzie and Pickett, 1984); D (Late Pleistocene Hengchun Limestone; Hu, 1979); E (Late Pleistocene Hengchun Limestone; Hu, 1981); F (Late Pleistocene Tungshiao Formation; Hu, 1986); G (Early Pliocene Maja Formation); H (Early Pleistocene Chinen Sand); I (Middle Pleistocene Shimajiro Formation); J (Early Pleistocene Sogwipo Formation and Middle Pleistocene Shinyangri Formation; Lee, 1990); K (Plio-Pleistocene Ananai Formation); L (Holocene Takahama shell bed); M (Holocene Hamamatsu Formation); N (Holocene bore hole core samples; Irizuki *et al.*, 1998); O (Plio-Pleistocene Omma Formation; Ozawa, 1996); P (Late Pleistocene Miyainu and Numashiro formations); Q (Pliocene Sawane Formation); R (Late Pleistocene Hamada Formation).

Figure 9. Juvenile specimens of *Loxoconcha japonica* species group. 1, 2. *Loxoconcha japonica* Ishizaki, 1968. 3, 4. *Loxoconcha shanhaiensis* Hu, 1981. 5, 6. *Loxoconcha tumulosa* (Hu, 1979). 7, 8. *Loxoconcha lilljeborgii* Brady, 1868. 1. A-1 stage carapace of same specimen in external left lateral view (a), dorsal view (b) and posterior view (c) from sample no. 8 (SUM-CO-1265), and hingement of the same stage of left valve (d) from sample no. 8 (SUM-CO-1266). 2. A-2 stage carapace of same specimen in external view (a-c) from sample no. 8 (SUM-CO-1267), and hingement of the same stage of left valve (d) from sample no. 8 (SUM-CO-1268). 3. A-1 stage carapace of same specimen in external view (a-c) from sample no. 20h (SUM-CO-1280), and hingement of the same stage of left valve (d) from sample no. 20h (SUM-CO-1281). 4. A-2 stage carapace of same specimen in external view (a-c) from sample no. 20h (SUM-CO-1282), and hingement of the same stage of left valve (d) from sample no. 20h (SUM-CO-1283). 5. A-1 stage carapace of same specimen in external view (a-c) from sample no. 23 (SUM-CO-1290), and hingement of the same stage of left valve (d) from sample no. 23 (SUM-CO-1291). 6. A-2 stage carapace of same specimen in external view (a-c) from sample no. 23 (SUM-CO-1292), and hingement of the same stage of left valve (d) from sample no. 23 (SUM-CO-1293). 7. A-1 stage carapace of same specimen in external view (a-c) from sample no. 19 (SUM-CO-1301), and hingement of the same stage of left valve (d) from sample no. 19 (SUM-CO-1302). 8. A-2 stage carapace of same specimen in external view (a-c) from sample no. 19 (SUM-CO-1303), and hingement of the same stage of left valve (d) from sample no. 19 (SUM-CO-1304). Scale bars = 100  $\mu$ m. (A for a-c; B for d)



**Figure 12.** Geographic distributions of four species of *Loxoconcha japonica* species group (Recent). a (Mauritius; Brady, 1868); b (Burma; Gramann, 1975); c (Sunda Shelf; Mostafawi, 1992); d (Hainan Island; Gou, 1990); e (Hong Kong); f (Manila Bay; Keij, 1954); g (Cebu Island); h (West Australian Coast; Hartmann and Hartmann, 1978); i (Lizard Island; Behrens, 1991); j (Guam); k (Truk); l (Marshall Islands); m (Gilbert Islands); n (Samoa); o (Tuamotu Islands; Hartmann, 1984); p (South Taiwan); q (Sekisei-sho); r (Miyako Island); s (Okinawa); t (Yoron Island); u (Tokuno-shima Island); v (Amami-o-shima Island); w (southern part of Korean Peninsula; Choe, 1984MS); x 1–17 (Japan coast; x6 = Uranouchi Bay; Ishizaki, 1968). e, g, and j–n (R. Ross, pers. comm., 2002).

from the Middle Pleistocene Shimo-jiro Formation from the Okino-erabu Island of the Ryukyus (Loc. I: Figure 2, loc. h). This species also occurs in two Late Pleistocene formations from Taiwan, the Hengchun Limestone (Locs. D and E: Figure 2, locs. 11 and 12) and the Tungshiao Formation (Loc. F: Figure 2, loc. k).

**Recent distribution** (Figure 12).—*L. lilljeborgii* is widely distributed over lower latitude coastal regions of the Indian Ocean (Locs. a and b), the South China Sea (Locs. d and f), the northern part of Australia (Locs. h and i) and the Ryukyus (Locs. s, t and v: Figure 2, locs. 17, 19 and 20). *L. tumulosa* is distributed over lower latitudes in the West Pacific coastal regions of the South China Sea (Locs. c, d and g), the northeastern part of Australia (Loc. i), many islands of the West Pacific (Locs. j–o), Taiwan (Loc. p: Figure 2, loc. 23), and the Ryukyus (Locs. s–u: Figure 2, locs. 18–20). *L. japonica* is distributed over lower-to middle latitude coastal regions from Hong Kong to Japan (Locs. e, q, s, t, u, v, w and x1–17: Figure 2, locs. 1–20 and 22). *L. shanghaiensis* is only distributed over the lower latitude coastal regions of Hainan Island (Loc. d), Taiwan (Loc. p: Figure 2, loc. 23) and the Ryukyus (Locs. q–t: Figure 2, locs. 17 and 19–22).

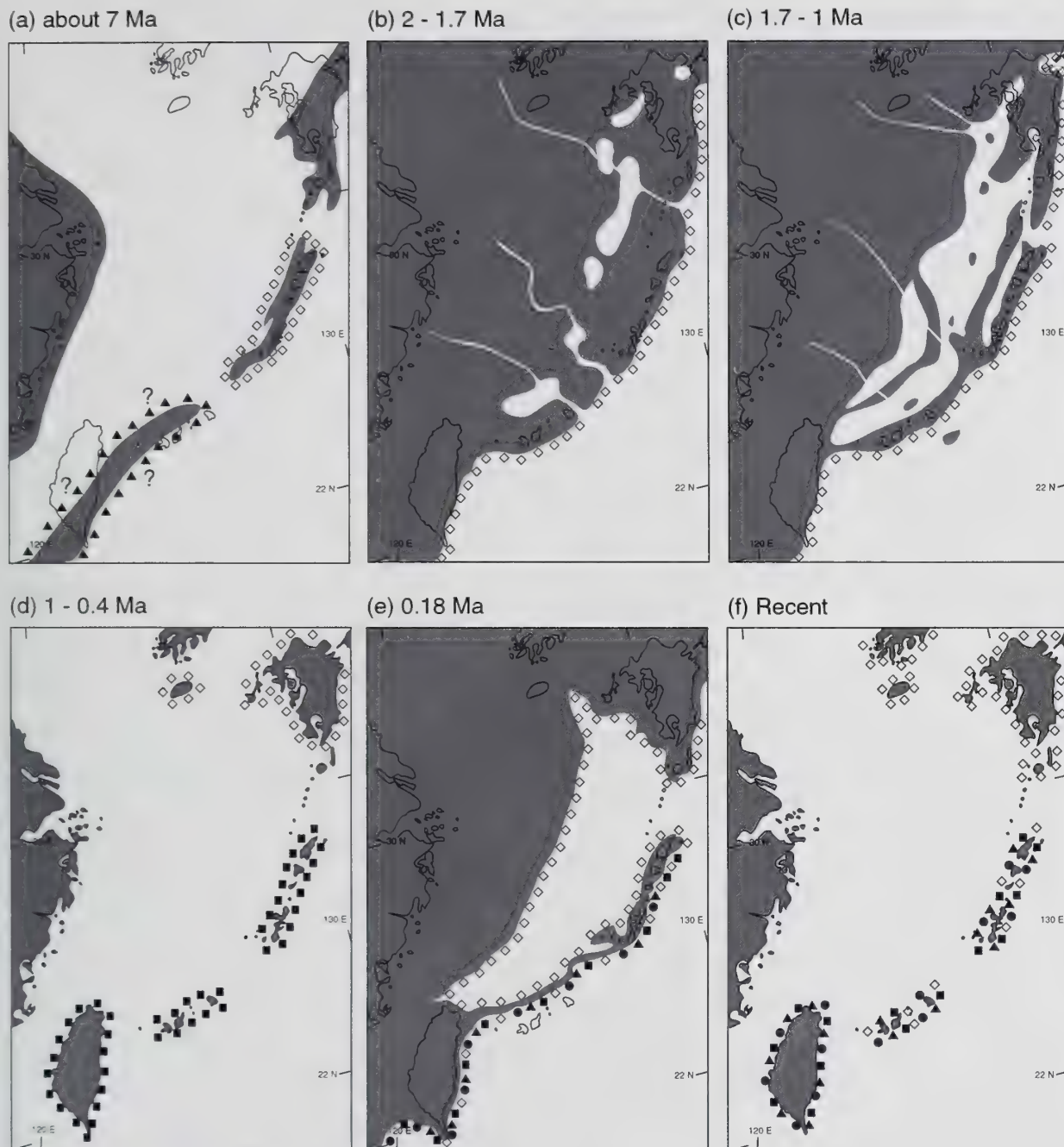
The dispersal and evolution of the four species can be in-

ferred from these data (Figure 13). Firstly, *L. lilljeborgii* and *L. tumulosa* were distributed over the Indian Ocean in the Late Miocene. Secondly, these species migrated from the Indian Ocean to the West Pacific Ocean during the Early Pliocene. Based on morphological and ontogenetic information, together with biogeographic data, *L. japonica* evolved from the northern population of *L. tumulosa*. Finally, *L. shanghaiensis* evolved from the southern population of *L. japonica* in the Middle Pleistocene. These inferences are discussed in greater detail below.

## Discussion

Paleobiogeographic and ontogenetic changes in the carapace morphology of the *L. japonica* species group from East Asia are the key to interpreting the phylogeny of the group. In the preceding section, we deduced that *L. japonica* evolved from *L. tumulosa* in the Early Pliocene. In *L. japonica*, the lateral outline and the surface ornamentation change in the A-1 instar and the A-2 instar, respectively. In contrast, in *L. tumulosa*, the lateral outline and the surface ornamentation change in the adult and the A-1 instar, respectively. Furthermore, in *L. japonica*, the alate ridge, which is a common character among the juvenile stages of





**Figure 13.** Paleobiogeographic distribution of *Loxoconcha japonica* species group around the Ryukyus. Shaded zones are land areas. *Loxoconcha japonica* Ishizaki, 1968 (open diamond shapes), *Loxoconcha shanhaiensis* Hu, 1981 (solid squares), *L. tumulosa* (Hu, 1979) (solid triangles) and *L. lilljeborgii* (solid circles). Paleogeographic reconstructions are after (a), Ujiié (1986); (b)–(d), Kimura (1996); (e), Ujiié and Nakamura (1996).

all four species, disappears in most adult specimens. From this evidence, the carapace characters of *L. japonica* are considered to have developed by peramorphosis. Moreover, it was deduced that *L. shanhaiensis* differentiated from *L. japonica* in the Middle Pleistocene. In *L. shanhaiensis*, ontogenetic changes of the lateral outline and

the surface ornamentation are delayed by one stage, and the adult stage retains the alate ridge. These data indicate that the carapace characters of *L. shanhaiensis* are derived from *L. japonica* by paedomorphosis.

A heterochronic process results from the modification of the relationships among three parameters—age, size and

shape—which are assumed to be independent (Gould, 1977). Peramorphosis and paedomorphosis are each subdivided into three processes, and heterochronic evolution is described by one or more of these six processes (Kluge, 1988). In many taxa, it is generally assumed that age is equivalent to size when dealing with fossils, but in fact the relationship between age and size is not always correlative. In the case of ostracods, each instar can be compared in relative age, but relative age does not always correspond to absolute age. If it is assumed that the relative age equals the absolute age, we can consider age and size to be independent of each other. We cannot decide which of the six processes can be applied to the heterochronic evolution of the *L. japonica* species group, because we lack information on the earliest ontogenetic stage of each species. Nonetheless, we can state that either peramorphosis or paedomorphosis has occurred. If the number of moltings is the same among the four species, then it is likely that *L. japonica* became differentiated from *L. tumulosa* by pre-displacement and *L. shanhaiensis* was derived from *L. japonica* by post-displacement. To solve these phylogenetic problems, it is essential to clarify the life history of the species in culturing experiments (Ikeya and Kato, 2000).

### Systematic descriptions

Order Podocopida G. W. Müller, 1894  
 Suborder Podocopina Sars, 1866  
 Superfamily Cytheracea Baird, 1850  
 Family Loxoconchidae Sars, 1925  
 Subfamily Loxoconchinae Sars, 1925  
 Genus *Loxoconcha* Sars, 1866

#### *Loxoconcha japonica* Ishizaki, 1968

Figures 3.1–3.3, 3.6; 5A, 5a; 7A; 9.1, 9.2

*Loxoconcha japonica* Ishizaki, 1968, p. 28, 29, pl. 2, fig. 1, pl. 6, figs. 10–12; Ishizaki, 1971, p. 86, pl. 3, fig. 21; Okubo, 1980, p. 416–418, figs. 12, 13, 18a–d; Hu, 1981, p. 77, pl. 3, fig. 7; Kamiya, 1988a, pl. 1, figs. 1–7, text-figs. 4, 5, 7, 8, 10, 11, 13; Kamiya, 1988b, pl. 1, figs. 1–6; Kamiya, 1988c, pl. 1, figs. 9–16; Kamiya, 1989a, pl. 1, figs. 1–8, 13, 14, 17, pl. 2, figs. 1–3, 10, text-figs. 1–8; Kamiya, 1989b, figs. 3, 4, 6, 7, 9, 11, 12; Ruan and Hao, 1988, p. 323, pl. 57, figs. 11–13; Lee, 1990, p. 358, pl. 34, figs. 3, 4; Ikeya and Suzuki, 1992, pl. 5, fig. 9; Kamiya and Hazel, 1992, figs. 1, 3, 4, pl. 1; Kamiya and Nakagawa, 1993, pl. 5, figs. 11, 12; Ozawa, 1996, pl. 6, fig. 5; Cao, 1998, pl. 3, figs. 16–19; Irizuki *et al.*, 1998, fig. 3–5; Yamane, 1998, pl. 6, fig. 2; Yasuhara and Irizuki, 2001, pl. 6, fig. 12.

*Loxoconcha impressa* (Baird). Kajiya, 1913, p. 9, pl. 1, figs. 50, 51.

**Table 2.** Measurements of valve of *Loxoconcha japonica* Ishizaki, 1969 from sample nos. 1, 6, 8 and 17. Abbreviations: Av = average; OR = observation range; N = number of specimens; M = male; F = female; R = right; L = left.

Sample (No.)	Sex	Valve	Length (mm)		Height (mm)		N
			Av.	OR	Av.	OR	
Suttu Bay (1)	M	R	0.65	0.63–0.67	0.45	0.43–0.46	15
	M	L	0.66	0.64–0.69	0.44	0.41–0.46	14
	F	R	0.58	0.55–0.62	0.42	0.40–0.45	27
	F	L	0.59	0.55–0.64	0.43	0.40–0.45	29
Kagoshima (6)	F	L	0.54	0.49–0.60	0.40	0.38–0.44	24
Misaki (8)	M	R	0.59	0.56–0.64	0.40	0.38–0.43	30
	M	L	0.60	0.57–0.64	0.40	0.37–0.44	36
	F	R	0.54	0.51–0.61	0.39	0.36–0.43	42
	F	L	0.55	0.52–0.61	0.40	0.37–0.44	46
Amami Is. (17)	M	R	0.59	0.55–0.64	0.40	0.37–0.43	30
	M	L	0.59	0.56–0.64	0.41	0.37–0.43	29
	F	R	0.54	0.49–0.58	0.38	0.35–0.41	58
	F	L	0.54	0.50–0.59	0.39	0.35–0.43	64

*Loxoconcha* sp. Hanai, 1961, p. 371, text-fig. 12, figs. 4a, b; Igo and Ikeya, 1971, p. 204, fig. 13.

*Loxoconcha* sp. A. Ishizaki, 1968, p. 34, pl. 7, figs. 4, 5; Ishizaki, 1971, p. 88, pl. 3, fig. 16.

? *Loxoconcha japonica* Ishizaki. Hu, 1979, p. 69–70, pl. 2, figs. 32–37, text-fig. 8; Hu, 1984, pl. 4, figs. 24–26; Cai, 1982, pl. 3, fig. 21.

Non *Loxoconcha japonica* Ishizaki. Hu, 1981, pl. 3, figs. 1–4, 8, text-fig. 14; Hu, 1983, pl. 2, figs. 3, 4, 6; Hu, 1986, pl. 4, figs. 22, 28, 30, 31; Nohara and Ohshiro, 1992, fig. 6.

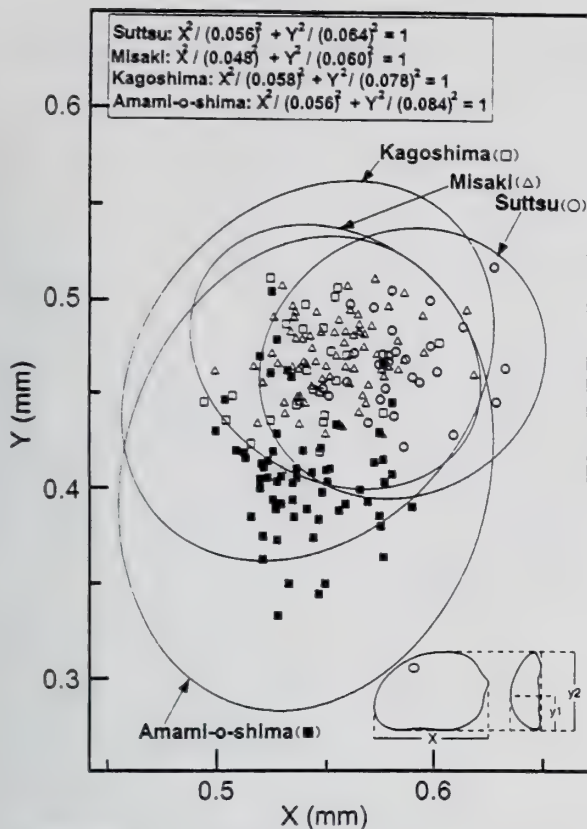
**Types.**—Holotype, a male left valve, IGPS coll. cat. no. 90260; paratypes, a male right valve, IGPS coll. cat. no. 90261, a female left valve, IGPS coll. cat. no. 90262.

**Type locality.**—St. 303 (33°24.6'N, 133°26.5'E), Urano-uchi Bay, Kochi Prefecture, Shikoku, Japan, Recent, coarse sand, depth 25 m (×6 in Figure 12).

**Diagnosis.**—Large sexual dimorphism; in lateral view, male more elongate and highest more posteriorly than the other three species described here from the *L. japonica* group. Carapace subrhomboidal in lateral view. Dorsal margin straight and sloped toward anterior in male, arched dorsally in female; anterior margin with an oblique infracurvature; ventral margin concave at mid-anterior portion; posterior margin broadly rounded at posteroventral portion. No prominent caudal process. In dorsal view, carapace diamond-shaped, often wedge-shaped in some females. In posterior view, carapace generally elliptical, often egg-shaped in female. Ornamentation consists of concentrically arranged reticulation. Boot-shaped male copulatory organ has trapezoidal basal capsule, triangular distal lobe and basally inflated L-shaped ductus ejaculatorius.

**Dimensions.**—Length and height of adult males and fe-





**Figure 14.** Geographic variation in posterior view of females of *Loxoconcha japonica* Ishizaki, 1968. Symbols refer to Suttsu population (open circles;  $n = 29$ ), Misaki population (open triangles;  $n = 76$ ), Kagoshima population (open squares;  $n = 24$ ) and Amami-o-shima population (solid squares;  $n = 63$ ). Plot of the distance from the base of ventral margin to the point on the marginal line of the maximum width ( $y_1$ )/height ( $y_2$ ) on the posterior view of left valve ( $Y = y_1/y_2$ ) versus length in the lateral view ( $X$ ), with series of rejection ellipses with 95% confidence intervals.

males from the sample nos. 1, 6, 8 and 17 are listed in Table 2.

**Occurrences.**—Fossil (Figure 11): Early Pliocene Maja Formation from Kume Island; Pliocene Sawane Formation from Sado Island; Late Pliocene Yonabaru Formation from Okinawa Island; Pleistocene formations and Holocene deposits and boring core samples from Honshu to Cheju Island, southern Taiwan and Hong Kong. Recent (Figure 12): Japan (Hokkaido-Iriomote Island), southern coast of Korean Peninsula and Hong Kong.

**Remarks.**—Some specimens from Recent material from the Ryukyus and fossils from the Ryukyus to Taiwan, have an alate ridge on the posteroventral area (see Ruan and Hao, 1988, pl. 57, fig. 13). The alate ridge is especially developed in southern female specimens with an egg-shaped outline in posterior view (Figure 14); this ridge is not developed in males. *L. impressa* reported by Kajiyama (1913) belongs to this species, based on carapace outline,

surface ornamentation and the shape of the male copulatory organ. In the illustration of the male copulatory organ by Okubo (1980) it appears that the distal part of the ductus ejaculatorius extends beyond from the illustrated figure. However, we think that his specimen has been crushed and modified in shape.

### *Loxoconcha shanhaiensis* Hu, 1981

Figures 4.1, 4.2, 4.5; 5B, 5b; 6; 7B; 9.3, 9.4

*Loxoconcha shanhaiensis* Hu, 1981, p. 76, 77, pl. 3, figs. 5, 9, 11, text-figs. 13a, b; Hu, 1982, p. 180, 182, pl. 2, fig. 23; Hu, 1984, pl. 4, figs. 21–23, 27.

*Loxoconcha japonica* Ishizaki. Hu, 1981, pl. 3, figs. 1–4, 8, text-fig. 14; Hu, 1983, pl. 2, figs. 3, 4, 6; Hu, 1986, pl. 4, figs. 22, 28, 30, 31; Nohara and Ohshiro, 1992, fig. 6.

**Types.**—Holotype, TNUM. 4148; paratypes, TNUM. 4151, 4153 and 4150.

**Type locality.**—The west margin of the Hengchun Table land, near Shanhai-li, 80–90 m above sea level, about 3 km west of Hengchun City, southern Taiwan (E in Figure 11).

**Diagnosis.**—In lateral view, carapace subtrapezoidal and ornamented by concentric coarse reticulations. Boot-shaped male copulatory organ has trapezoidal basal capsule, subtriangular distal lobe, a shoehorn-shaped ductus ejaculatorius and a triangular clasping apparatus.

**Description.**—**Carapace:** Strong sexual dimorphism. Carapace subtrapezoidal, highest at posterior cardinal angle in lateral view. Dorsal margin straight and sloped toward anterior; anterior margin with an oblique curvature and well developed denticulations; ventral margin straight; posterior margin with broad flat zone, broadly rounded in posteroventral area, with several strong spines. Short but prominent caudal process. In dorsal view, carapace wedge-shaped with maximum width about one-third of length from posterior end. Ornamentation consists of concentrically arranged coarse reticulation. Prominent alate ridge developed in posteroventral area extended toward posterior. **Pore system:** (a) Lateral (sieve-type) pore system. 67 pores distributed on each valve in adult specimens. (b) Marginal pore system includes 16 pores (Figure 5b). **Hinge** (Figure 4.5a, b): Gongylodont. Hinge-line nearly straight. In left valve, anterior element is a downturned claw, median element has 39–42 teeth, and posterior element is a ball-like knob. The hinge of the right valve is complementary. **Muscle scars** (Figure 4.5a, b): Row of 4 adductor muscle scars curved anteriorly at inside of median to slightly anterior of ventromedian of carapace. The upper of the two middle ones elliptical with hollows at middle, the other three scars bean-shaped. Elliptical frontal scar inclines anteroventrally in front of middle two scars. Two divided mandibular scars in front

of lowest adductor muscle scars. Fulcral point absent. **Marginal infoldment** (Figure 5b): Widest in anteroventral region, twisted in middle of ventral region and narrowed posterodorsally. **Appendages**: Antennule (Figure 6A). Five segments (there are six segments, but 4th and 5th are fused). Length ratio between distal segments is 26:19:8:29:19. Costae well developed in 2nd, 3rd and 4th segments. Second segment has numerous short hairs on the anterior margin and a short seta on the posterior margin. Third segment has a short seta on the anterior distal end. Fourth segment has two short and three long setae. Fifth segment with four long setae on the distal end. **Antenna** (Figure 6B): Four articulated segments (there are five segments actually, but the 3rd and 4th are fused). Length ratio between distal segments is 26:11:46:4. Costae well developed, especially broad in the anterior margin of 3rd segment. Second segment has a long two-segmented exopodite and a seta on the posterior margin. Third segment has a pair of unequal long setae and numerous hairs on the anterior margin one-sixth of the distance from the proximal end. Along the posterior margin of the 3rd segment, three unequal-sized long setae and numerous hairs are developed in the middle of the ledge and one-third of the distance from the distal end. Furthermore, the third segment bears a seta on the posterior distal end. Fourth segment has two very well developed terminal claws with numerous serrations. **Mandible** (Figure 6C): Five-segmented. Length ratio between two propodite segments and three endopodite segments is 25+: 16:8:12:5. Basal segment (coxa) with eight teeth and a seta on anterior distal margin. Second segment of protopodite (basis) bears an exopodite reduced to a seta. First and 2nd segments of endopodite almost fused. First segment of endopodite with two long setae on the ventral distal end. Second segment of endopodite with a pair of setae on the proximal and ventral distal ends, respectively. Furthermore, the 2nd segment has two setae on the anterior dorsal margin and a seta on the anterior distal margin. Third segment of endopodite with three pairs of setae on the distal end. **Maxilla** (Figure 6D): Extremely thin branchial plate (exopodite) with 16 setae. Basal segment bears a palp and three masticatory processes. Palp indistinctly two-segmented. The proximal segment bears 4 setae on its anterior distal end. Distal segment with three setae on the distal end and one seta on the ledge in the posterior proximal end. Outer, middle and inner masticatory processes bear 5, 4 and 5 setae, respectively, on each distal end. **Thoracic legs** (Figure 6E, F and G): All three legs are 4-segmented, similar in shape. Length ratio between distal segments is 24:20:8:13 in 3rd thoracic leg. Costae developed on both margins. First segment having a seta on the anterior proximal end and two setae on the anterior proximal end. The segment has a seta on the posterior proximal

**Table 3.** Measurements of valve of *Loxoconcha shanhaiensis* Hu, 1981 from sample nos. 17 and 20. Abbreviations same as Table 2.

Sample (No.)	Sex	Valve	Length (mm)		Height (mm)		N
			Av.	OR	Av.	OR	
Amami Is. (17)	M	R	0.48	0.45–0.51	0.33	0.31–0.37	29
	M	L	0.49	0.46–0.54	0.33	0.31–0.36	27
	F	R	0.48	0.46–0.52	0.34	0.32–0.36	26
	F	L	0.48	0.44–0.53	0.34	0.31–0.37	42
Okinawa Is. (20)	M	L	0.50	0.44–0.52	0.33	0.32–0.34	12
	F	L	0.49	0.46–0.53	0.34	0.32–0.38	40

end. Second segment bearing numerous hairs along the anterior margin and a seta on the anterior distal end. Third and 4th segments bearing numerous hairs along the anterior margin. **Copulatory organ** (Figure 7B): The basal capsule, with costae in the margin, is trapezoidal. A large subtriangular distal lobe and a small clasping apparatus are developed on the distal end of the basal capsule. Small shoehorn-shaped ductus ejaculatorius.

**Dimensions.**—Length and height of adult males and females from the sample nos. 17 and 20 are given in Table 3.

**Occurrences.**—Fossil (Figure 11): Middle Pleistocene Shimo-jiro Formation from Okino-erabu Island; Late Pleistocene Tungshiao Formation and Hengchun Limestone from Taiwan. Recent (Figure 12): Ryukyus (Amami Island to Iriomote Island), Taiwan and Hainan Island.

**Remarks.**—Specimens reported by Hu (1981, 1983, 1986) and Nohara and Ohshiro (1992) as *L. japonica* have coarse reticulation, straight dorsal margin sloped toward the anterior, posterior margin with broad flat zone and several strongly developed spines, so these specimens are identified as *L. shanhaiensis*.

### *Loxoconcha tumulosa* (Hu, 1979)

Figures 4.3, 4.4, 4.6; 5C, 5c; 9.5, 9.6

*Loxocorniculum tumulosum* Hu, 1979, p. 71, 72, pl. 2, figs. 17, 21, 22, 26, 27, 30, 31, text-fig. 10.

*Loxoconcha tumulosa* (Hu). Hu, 1981, p. 78, pl. 3, figs. 6, 7; Hu, 1984, pl. 4, figs. 17, 18, 20; Zhao *et al.*, 1985, pl. 20, fig. 11; Gou, 1990, p. 25, pl. 3, figs. 45–47.

*Loxoconcha alata* Brady. Guha, 1968, p. 61, pl. 4, figs. 5, 13.

*Loxoconcha heronislandensis* Hartmann. Hartmann, 1984, p. 128, pl. 7, figs. 1–6, text-figs. 47, 48; Whatley and Zhao, 1987, p. 350, pl. 5, fig. 12; Behrens, 1991, pl. 5, figs. 5, 6.

*Loxoconcha* sp. Hartmann and Hartmann, 1978, pl. 10, fig. 6.

Non *Loxoconcha tumulosa* (Hu). Zhao and Wang, 1988, pl. 2, fig. 27.

**Types.**—Holotype, TUM. 4033; paratypes, TUM. 4034–4036, 4065, 4066.

**Type locality.**—A road cut from Hengchun to Oluanpi, 15–20 m above sea level, about 1 km east of Nanwan,



**Table 4.** Measurements of valve of *Loxoconcha tumulosa* (Hu, 1979) from sample no. 23. Abbreviations same as Table 2.

Sample (No.)	Sex	Valve	Length (mm)		Height (mm)		N
			Av.	OR	Av.	OR	
Taiwan (23)	F	R	0.51	0.50–0.53	0.33	0.33–0.34	10
	F	L	0.52	0.50–0.54	0.35	0.34–0.36	7

Pingtung Prefecture, southern Taiwan (D in Figure 11).

**Diagnosis.**—Large sexual dimorphism; in lateral view, male more elongate. Carapace rhomboidal in lateral view. Dorsal and ventral margins nearly parallel; anterior margin with an oblique infracurvature, and developed denticulations; posterior margin broadly rounded in posteroventral area. Prominent caudal process. In dorsal view, carapace wedge-shaped. In posterior view, carapace egg-shaped. Ornamentation consists of very coarse concentrically arranged reticulation. Prominent alate ridge developed at postero-ventral area, and protuberance developed in posterodorsal area.

**Dimensions.**—Length and height of adult males and females from the locality sample no. 23 is listed in Table 4.

**Occurrences.**—Fossil (Figure 11): Late Miocene Round Chalk and Silt Formation, Pliocene Guiter Formation from the Andaman Islands of the Indian Ocean and Late Pleistocene Hengchun Limestone from Taiwan. Recent (Figure 12): Ryukyus (Tokuno-shima to Okinawa), Taiwan, Hainan, Cebu Island, Lizard Island, Guam, Truk, Marshall Islands, Gilbert Islands, Samoa and Tuamotu Islands from Southwest Pacific.

**Remarks.**—Specimens reported by Guha (1968) from the Late Miocene and the Pliocene sediments of Interview Island and Guiter Island as *L. alata* are identified as *L. tumulosa*. *L. heronislandensis* reported by Behrens (1991) also belongs to this species. A specimen reported by Zhao and Wang (1988) as *L. tumulosa* differs from this species, because it has a protruded anterior margin and does not have a posterodorsal protuberance.

### *Loxoconcha lilljeborgii* Brady, 1868

Figures 3.4, 3.5, 3.7; 5D, 5d; 7C; 9.7, 9.8

*Loxoconcha lilljeborgii* Brady, 1868, p. 183, pl. 13, figs. 11–15; Mostafawi, 1992, p. 151, pl. 5, fig. 102.

*Loxoconcha lilljeborgii* Brady? Whatley and Zhao, 1987, p. 351, pl. 5, fig. 13.

*Loxoconcha lilljeborgii* Brady. Keij, 1954, p. 358, pl. 3, fig. 4; Guha, 1968, p. 61, pl. 4, fig. 20; Gramann, 1975, pl. 5, figs. 6–8; Zhao *et al.*, 1985, pl. 20, fig. 12; Zhao and Wang, 1988, pl. 2, fig. 26.

*Loxoconcha georgei* Hartmann and Hartmann, 1978, p. 105, pl. 9, figs. 15, 16, text-figs. 259–268, (non) pl. 9, figs. 13, 14; Howe and McKenzie, 1989, p. 24, figs. 8, 84, 85, 154;

**Table 5.** Measurements of valve of *Loxoconcha lilljeborgii* Brady, 1868 from sample no. 17. Abbreviations same as Table 2.

Sample (No.)	Sex	Valve	Length (mm)		Height (mm)		N
			Av.	OR	Av.	OR	
Amami Is. (17)	M	R	0.51	0.47–0.54	0.34	0.32–0.36	78
	M	L	0.52	0.49–0.55	0.34	0.32–0.36	69
	F	R	0.50	0.46–0.54	0.34	0.32–0.39	95
	F	L	0.50	0.45–0.54	0.35	0.31–0.37	97

Behrens, 1991, p. 116, 117, pl. 4, figs. 6–9.

*Loxoconcha broomensis* Hartmann and Hartmann, 1978, p. 106, pl. 10, fig. 1, text-figs. 272, 279, (non) pl. 10, figs. 2–4, text-figs. 269, 280.

*Loxocorniculum* sp. 1, Tabuki *et al.*, 1987, pl. 2, fig. 11; Tabuki and Nohara, 1990, pl. 2, fig. 11; Tabuki, 1992, pl. 1, fig. 15.

*Loxocorniculum* sp. A. Tabuki and Nohara, 1988, pl. 1, figs. 13, 14.

*Loxocorniculum* cf. (*Loxoconcha*) *georgei* Hartmann. Tabuki and Nohara, 1995, fig. 4–8.

*Loxocorniculum georgei* (Hartmann). Gou, 1990, p. 26, pl. 3, figs. 43, 44.

**Types.**—Not defined.

**Type locality.**—Mauritius, Indian Ocean (a in Figure 12).

**Diagnosis.**—Strong sexual dimorphism; in lateral view, male more elongate. Carapace subrhomboidal in lateral view. Dorsal margin nearly straight in male, arched dorsally in female; anterior margin with an oblique infracurvature; ventral margin concaved in mid-anterior area; posterior margin broadly rounded in posteroventral area. Caudal process not prominent. In dorsal view, carapace elongate arrowhead-shaped. In posterior view, egg-shaped. Ornamentation consists of concentrically arranged oblong pits. Prominent protuberance developed in posterodorsal area. Pear-shaped male copulatory organ has inflated trapezoidal basal capsule, subtriangular distal lobe, a leaf-shaped clasping apparatus and elongate ductus ejaculatorius.

**Dimensions.**—Length and height of adult males and females from the sample No. 17 is given in Table 5.

**Occurrences.**—Fossil (Figure 11): Late Miocene Round Chalk and Silt Formation, Pliocene Guiter Formation from the Andaman Islands of the Indian Ocean, and Late Pleistocene Hengchun Limestone from Taiwan. Recent (Figure 12): Ryukyus (Tokuno-shima to Okinawa), Taiwan, Hainan, and Lizard Island from Southwest Pacific.

**Remarks.**—Specimens reported from the Ryukyus as *Loxocorniculum* sp. 1 (by Tabuki *et al.*, 1987; Tabuki and Nohara, 1990; Tabuki, 1992), *Loxocorniculum* sp. A (by Tabuki and Nohara, 1988) and *Loxocorniculum* cf. (*Loxoconcha*) *georgei* (Tabuki and Nohara, 1995) are identified as *L. lilljeborgii*, with its carapace outline, concentri-

cally arranged oblong pits and postero-dorsal alate ridge. Hartmann and Hartmann (1978) described *Loxoconcha georgei* as a new species, and figured carapaces of both sexes and male soft parts, but a type specimen was not designated. Judging from the carapace ornamentation, we think the figured male and female specimens belong to different species. The male specimens we identify as *L. lilljeborgii*, with its concentrically arranged oblong pits, nearly straight dorsal margin, developed posterodorsal alate ridge and identically shaped of male copulatory organ. On the other hand, the female specimens are *Loxoconcha broomensis*, which was described in the same paper. This specimen has two strong anterior ridges. Carapaces of both sexes and the male soft parts of *L. broomensis* were also figured by Hartmann and Hartmann (1978), but a type specimen was not designated. Judging from the carapace outline and ornamentation, the female specimen should be identified as *L. lilljeborgii*.

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*Note added in proof.*—After the acceptance of the manuscript, T. Kase (National Science Museum, Tokyo) kindly provided us specimens of *Loxoconcha lilljeborgii* from the Tartaro Formation (Late Miocene) of Luzon Island, Philippines. The fossil record of *L. lilljeborgii* in East Asia, therefore, dates back from the Pleistocene to the Late Miocene.



# Middle Permian (Guadalupian) brachiopods from the Xiujimqinqi area, Inner Mongolia, northeast China, and their palaeobiogeographical and palaeogeographical significance

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**Abstract.** A small brachiopod fauna is described from the lower part of the Xiujimqinqi Formation of the Xiujimqinqi area in central-east Inner Mongolia, northeast China. The age of this fauna is regarded as Wordian (Middle Guadalupian, Middle Permian) by comparison with a similar brachiopod fauna from the Zhesi area of central Inner Mongolia, and by constraints from fusulinaceans associated with the Zhesi fauna. The Xiujimqinqi fauna is typical of mixed Boreal/Palaeoequatorial Middle Permian brachiopod faunas of East Asia. The mixed nature of these faunas is interpreted to have resulted from the combined effects of a middle palaeolatitudinal position, intensified plate convergence between Sino-Korea and Mongolia, and sea surface current connections with both the Arctic Sea in the north and eastern Palaeo-Tethys to the south. Possible *Kaninospirifer* is reported for the first time from China.

**Key words:** brachiopods, Middle Permian, northeast China, palaeobiogeography, transitional fauna, Xiujimqinqi

## Introduction

Permian marine sedimentary rocks are common in Inner Mongolia and contain abundant and varied marine invertebrate faunas. Generally, these faunas show a consistent palaeobiogeographical pattern, in that those from northern Inner Mongolia appear to be dominated by elements characteristic of the cool- to cold-water Boreal Realm, while faunas in central and southern Inner Mongolia tend to be more characteristic of the warm-water Palaeoequatorial Realm, but at the same time contain some taxa common to, or characteristic of, the Boreal or Gondwanan Realms (Tazawa, 1991; Shi *et al.*, 1995; Shi and Zhan, 1996). As such, the Permian marine faunas of central and southern Inner Mongolia typify a transitional biogeographical zone between the Boreal Realm to the north and the Palaeoequatorial Realm to the south, as defined and discussed by Shi *et al.* (1995).

Despite their ubiquity and abundance in the Permian marine sediments in Inner Mongolia and hence great significance for dating and correlation, only a few brachiopod faunas have been systematically described in detail. One of the better studied areas is the Xiujimqinqi area in central-eastern Inner Mongolia (Figure 1), where Permian brachiopods are common throughout the entire Lower and Middle Permian marine volcanoclastic, bioclastic and terrigenous sediments, well over 4,000 m in total thickness (Figure 2). Permian brachiopod faunas from various localities of this area have been studied by Lee *et al.* (1982, 1983, 1985) and Liu and Waterhouse (1985), and have furnished the basic premise for the Permian biostratigraphical zonation schemes of this area (Lee *et al.*, 1982, 1983; Liu and Waterhouse, 1985; BGMNG, 1991).

However, with the exception of Liu and Waterhouse's (1985) work, which described five brachiopod assemblages but did not give specific details on the exact location of



**Figure 1.** Map showing the study area, as well as the Zhesi area also referred to in the text. The enlarged map shows the detailed location of the area of study (Yuejin Coal Mine) in the Xiujimqinqi area. The shaded area in the index map is the Nei Mongol (Inner Mongolia) Autonomous Region.

their measured sections other than the general Xiujimqinqi area, the other earlier studies (Lee *et al.*, 1982, 1983, 1985) dealt only with certain taxa instead of the entire faunas. These latter investigations demonstrate that there are at least 10 relatively well exposed sections/localities in the general Xiujimqinqi area where Permian marine sequences with abundant brachiopods crop out. Lee *et al.* (1982) provided a detailed list of all the Permian brachiopod species then known to occur in this area, which they used as the basis for the erection of their brachiopod-based stratigraphical assemblages.

The present study is based on a small collection from the Yuejin Coal Mine, about 10 km southwest of Xiujimqinqi Township (Figure 1). This collection was originally made by the officers of the Bureau of Geology and Mineral Resources of Nei Mongol (Inner Mongolia) during the 1950s-1970s and was entrusted to Zhan Li-Pei, Chinese Academy of Geological Sciences (Beijing), for age determination. Zhan Li-Pei subsequently fulfilled this request by providing a list of his identified species and a broad age indication ["Early Permian", which, in terms of Jin's *et al.* (1997) proposed Permian timescale, includes both Early and Middle Permian]. Up to the present, this collection has not yet been systematically described. As will be documented below, this collection provides additional and

new records to what is currently known about the Middle Permian brachiopod faunas of the Xiujimqinqi area. Moreover, this collection also affords important material to document *Kaninospirifer* from China for the first time.

Specimens described and illustrated in this paper are housed in the Museum of Victoria, Melbourne, Australia, with registration numbers prefixed with NMVP.

### Stratigraphy

Over the last 2 decades, there has been a significant increase of lithostratigraphical names applied to the Permian rocks of the Xiujimqinqi area. In the two latest attempts to rationalize the stratigraphical nomenclature for the Permian System for the broad Inner Mongolian province (BGMNM, 1991; Jin *et al.*, 2000), many of the previously used names have been abandoned or treated as synonyms of others. In this study, we follow the stratigraphical framework recommended by BGMNM (1991) for the Xiujimqinqi area, which was also adopted in Jin *et al.* (2000). According to this scheme, the Permian sequence in the Xiujimqinqi area comprises, in ascending order, the Gegenaobao, Xiujimqinqi and Linxi formations (Figure 2). The Gegenaobao Formation is a sequence of acidic to intermediate volcanics, volcanoclastics and a minor amount of carbonate rocks. Both shallow marine and nonmarine fossils occur in this formation, indicating a volcanically active continental marginal marine setting. Among the marine fossils, brachiopods are most common and notably include species of *Jakutoproductus* and *Licharewia* (or *Tumarinia*). The cooccurrence of these two genera in this formation would indicate a relatively broad age range for the formation, from probably Artinskian (Early Permian) to as high as Roadian (early Middle Permian).

The Gegenaobao Formation in the Xiujimqinqi area is conformably overlain by the Xiujimqinqi Formation. The latter is dominated by andesite in the lower part, limestone and mudstone in the middle part, and siltstone in the upper part (Figure 2). Brachiopods occur throughout the formation but are mainly concentrated in several major horizons, each of which appears to form a distinct assemblage (Figure 2). By reference to the lithology and overall species composition, the brachiopod collection described below is considered to have come from the lower portion of the middle part of the formation. Plant fossils have also been reported from the siltstone beds in the upper part (BGMNM, 1991). As will be detailed below, the age of this formation is regarded as Wordian by correlation with faunas elsewhere.

Upwards, the Xiujimqinqi Formation grades to sandstone and conglomerate of the Linxi Formation without distinct discordance. The latter contains abundant Late Permian (Lopingian) mixed Cathaysia/Angara type flora



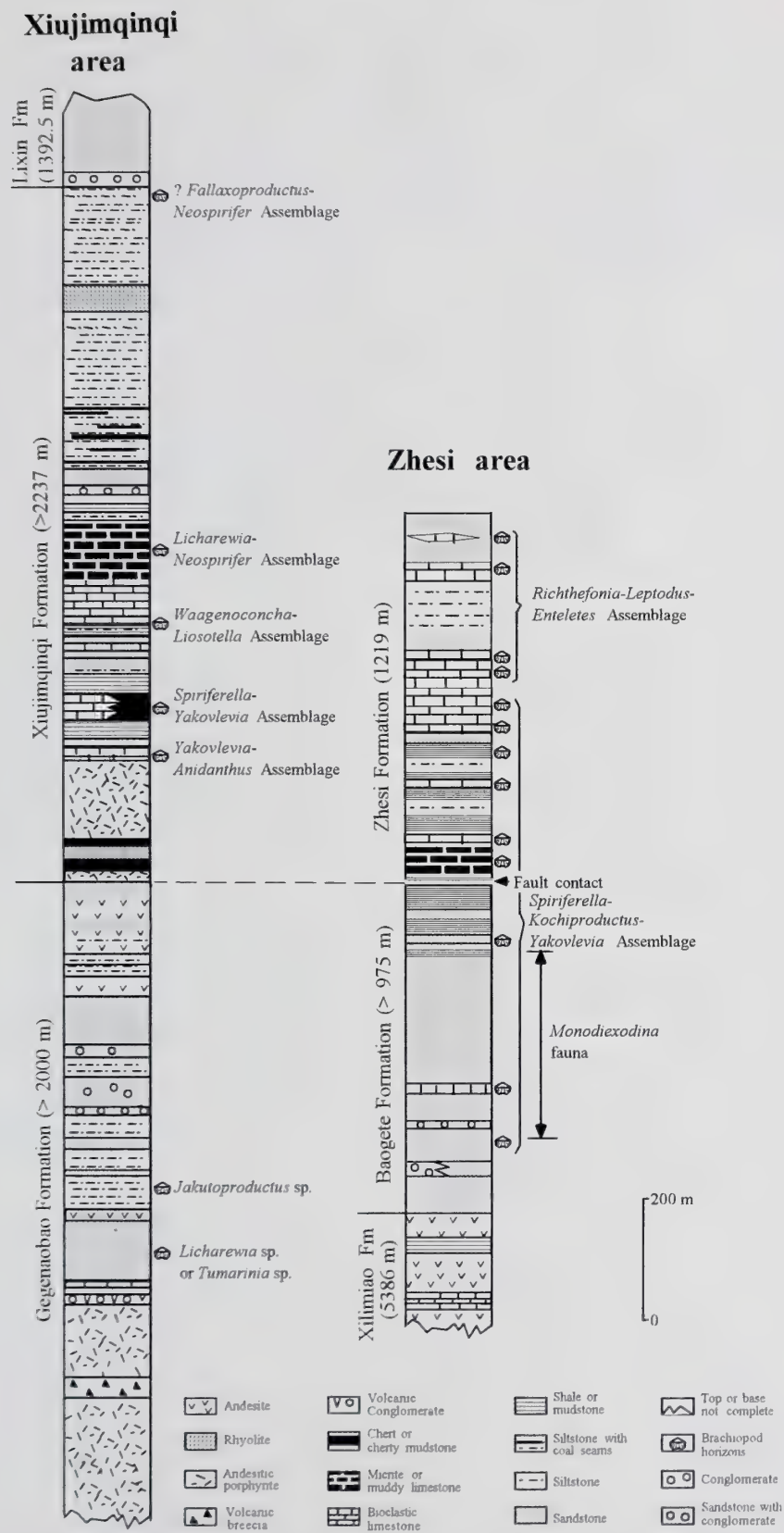


Figure 2. Permian stratigraphical sequences of the Xiujimqinqi and Zhesi areas, Inner Mongolia, northeast China. The stratigraphic columns and biozones are based on data from BGMNM (1991).

(Zhang, 1988).

### Correlation and age

The present collection comprises 10 species, of which several are species indeterminate and two genera and species indeterminate. At first glance, the assemblage cannot be readily correlated with any of the five assemblages originally established by Lee *et al.* (1982, 1983, 1985) and elaborated by BGMNM (1991) (see Figure 2) because of the lack of key zonal species in our collection; neither can it be matched with certainty with any of the five Early and Middle Permian brachiopod assemblages recognized by Liu and Waterhouse (1985). The closest assemblage among the established schemes is the *Spiriferella-Yakovlevia* assemblage of Lee *et al.* (1982), which occurs in the lower portion of the middle part of the Xiujiminqi Formation (Figure 2). This assemblage was originally recognized based on the brachiopod fauna from a limestone quarry about 7 km northwest of the present Yuejin Coal Mine (Lee *et al.*, 1982), and is characterized by abundant occurrence of *Spiriferella* and *Yakovlevia*, the former being represented by two species and the latter by four (Lee *et al.*, 1982). Other characteristic species of this assemblage include *Liosotella septentrionalis* (Tschernyshev), *Marginifera gobiensis* Chao, *Paramarginifera zhesiensis* Lee and Gu, *Waagenoconcha permocarbonica* Ustritskiy, *W. xiuqiensis* Lee, Gu and Li, *Strophalosia paradoxa* Fredericks, *S. pulchra* Lee, Gu and Li, *Linoproductus cora* (d'Orbigny), *Leptodus* sp., *Neospirifer xiujiuqinqiensis* Lee, Gu and Li, *N. ravana* (Diener), *N. moosakhailensis* (Davidson), and *Paeckelmanella laevis* Lee and Gu. Although lacking many of these species, the present collection nevertheless contains relatively abundant *Spiriferella* and neospiriferids (*Neospirifer* and *Kaninospirifer*), hence suggesting a significant degree of correlation. On the other hand, we note that some other factors, for example, insufficient sampling in the present collection and/or localized specialization of biofacies, may have also contributed to the apparent difference in species composition between the present collection and the *Spiriferella-Yakovlevia* assemblage.

The age of the above *Spiriferella-Yakovlevia* assemblage has been considered to be either late Early Permian (Lee *et al.*, 1982) or middle Early Permian (BGMNM, 1991) in the traditional twofold Permian chronostratigraphical timescale of China (e.g., Zhan and Li, 1984). A more specific age determination for the *Spiriferella-Yakovlevia* assemblage is possible by correlation with the classic Permian brachiopod faunas of the Zhesi area in central Mongolia (see index map in Figure 1 for location), where brachiopods are associated with fusulinaceans. Here, the Permian is divided into three formations: the Xilimiao Formation, Baogete Formation and Zhesi Formation, in as-

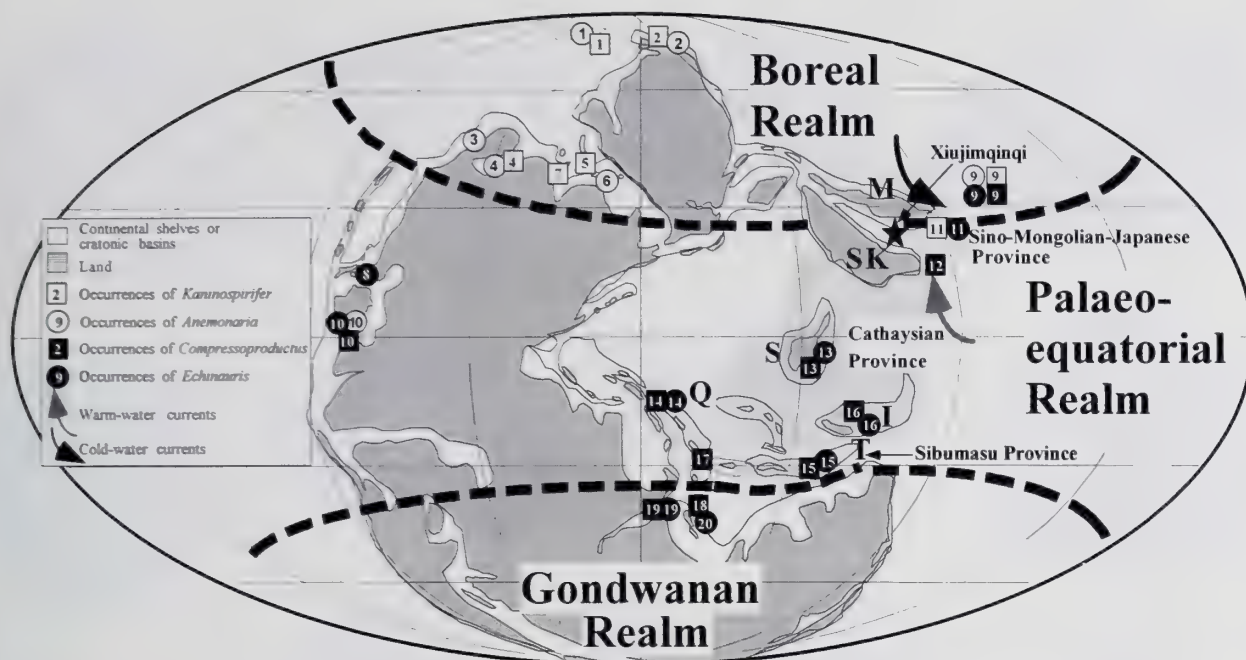
cending order (BGMNM, 1991) (Figure 2). The brachiopod-bearing horizons that are comparable with those of the Xiujiminqi area lie in the Baogete and Zhesi formations. Permian brachiopods are very rich in this area and have been the subject of two major monographical studies (Grabau, 1931; Duan and Li, 1985). According to them, the Permian brachiopods in this section can be divided into two broad assemblages: the *Spiriferella-Kochiproductus-Yakovlevia* assemblage (or SKY assemblage, as called by Duan and Li, 1985), followed by the *Richthofenia-Leptodus-Enteleles* assemblage (or RLE assemblage). Of these, the SKY assemblage is well correlated with the *Spiriferella-Yakovlevia* assemblage of the Xiujiminqi area as both assemblages contain abundant Boreal-type genera such as *Neospirifer*, *Spiriferella* and *Yakovlevia*, and are similarly characterized by an admixture of Boreal and Palaeoequatorial taxa. The RLE assemblage of the Zhesi area, on the other hand, is dominated by Palaeoequatorial or Cathaysian-type genera and bears no significant similarities with any of the Xiujiminqi assemblages.

The age of the SKY assemblage of the Zhesi section is well constrained by the associated fusulinaceans of the *Monodioxodina sutchanica* Zone in its lower part, and the fusulinaceans of the *Codonofusiella* Zone and corals of the *Waggenophyllum-Wentzella* Zone that directly and conformably overlie the SKY assemblage and are associated with the brachiopods of the RLE assemblage (Duan and Li, 1985; BGMNM, 1991) (Figure 2). The *Monodioxodina sutchanica* Zone is generally regarded as of early Midian or Wordian age (Kotlyar *et al.*, 1999; Shi and Tazawa, 2001), and the *Codonofusiella* and *Waggenophyllum-Wentzella* zones of Capitanian age (Jin *et al.*, 1997). Thus, the SKY assemblage can be safely assigned to the Wordian in age. This implies that the *Spiriferella-Yakovlevia* assemblage, and hence, by correlation, the present collection from the Yuejin Coal Mine under discussion, is also Wordian in age.

### Palaeobiogeographical and palaeogeographical implications

In spite of its small species composition, the present collection demonstrates aspects of a mixed Boreal/Cathaysian palaeobiogeographical fauna. The cool-water Boreal aspect of the fauna is represented by two characteristic northern Eurasian genera: *Anemonaria* and *Kaninospirifer*. *Anemonaria* is primarily restricted to the Arctic region (Arctic Russia, Spitsbergen, Greenland, and Arctic Canada) (Sarytcheva, 1977), although some occurrences from Australia (Briggs, 1998) and middle-latitude regions are also known, such as Japan (Tazawa and Niigata Pre-Tertiary Research Group, 1999; Tazawa, 2001) and the Russian Far East (Likharev and Kotlyar, 1978). The only exception to this essentially high-to middle-palaeolatitude





**Figure 3.** A Permian reconstruction map showing the distribution of *Anemonaria*, *Compressoproductus*, *Echinauris*, and *Kaninospirifer*, and the inferred palaeo-position (indicated by star) of Xiujimqinqi during the Middle Permian (base map from Ziegler *et al.*, 1998). Locations of the occurrences of *Anemonaria*, *Compressoproductus*, *Echinauris*, and *Kaninospirifer* are as follows: 1, Kolyma Block, Russia; 2, northern Verkhoyansk, Russia; 3, Yukon Territory, Canada; 4, Sverdrup Basin, Canada; 5, Kanin Peninsula, Russia; 6, Pechora Basin, Russia; 8, Phosphoria Basin, western USA; 9, Xiujimqinqi and adjacent areas in northeast China; 10, Texas, USA and central America; 11, SW Japan and South Primorye of Far Eastern Russia; 12, South Kitakami, northeast Japan; 12, South China 14, northwest Iran and Armenia; 15, Shan-Thai (Sibumasu) block; 16, Indochina; 17, southeast Pamir, Karakorum and central Afghanistan; 18, southern Tibet; 19, northwest Nepal; 20, Salt Range, Pakistan. Explanations of main tectonic blocks: Q, Qiangtang Block; I, Indochina Block; M, Mongolia Block; S, South China Block; SK, Sino-Korea Block; T, Shan-Thai (Sibumasu) Block.

dinal distributional pattern is a record of the genus from Texas, southern U.S.A. (Cooper and Grant, 1969, 1975) and Venezuela (Hoover, 1981). These two "outlying" occurrences may be explained by the possible effect of a California-type cold current that might have intermittently operated off the western coast of northern Pangea during the Permian, bringing cold-water Boreal faunal elements to palaeoequatorial Texas and South America (Shi, 1995; Shi and Tazawa, 2001).

By contrast, the palaeogeographical distribution of *Kaninospirifer* is much more restricted, with occurrences known only from the northern part of the Russian Platform, Arctic Canada, Greenland, and Spitsbergen (Kalashnikov, 1996), Mongolia (Pavlova, 1991), northeast China (this report) and Japan (Tazawa, 2000; see discussion below) (Figure 3).

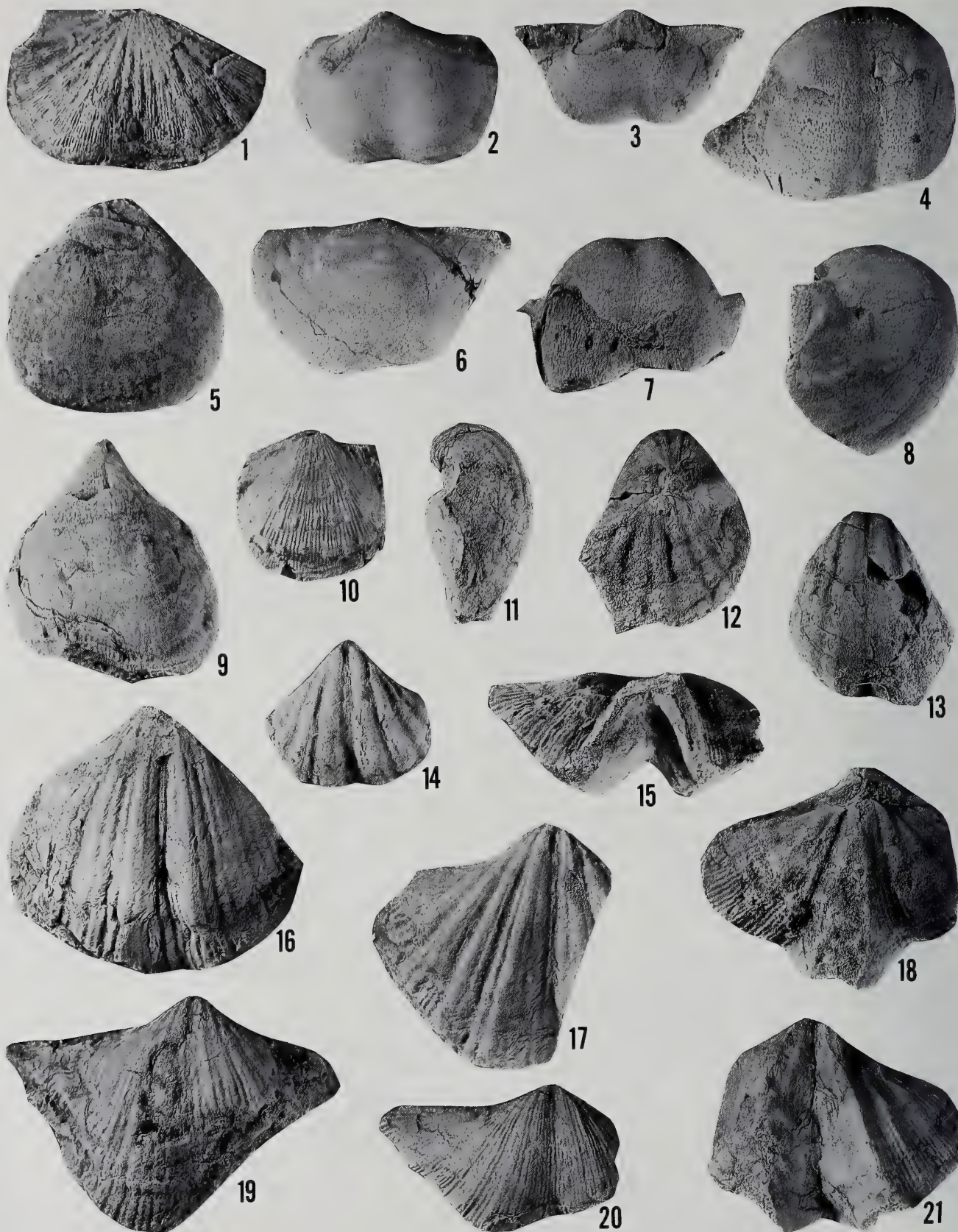
The warm-water palaeoequatorial aspect of the Xiujimqinqi brachiopod fauna is signaled by *Compressoproductus* and *Echinauris*. These two genera have essentially concordant palaeogeographical distributions, with occurrences restricted to the Tethys and south-west U.S.A. and have never been recorded from either the

Gondwanan Realm or the Boreal Realm proper (Figure 3).

In addition to the four genera noted above, the palaeogeographical distribution of *Spiriferella* is also of great interest. Unlike *Anemonaria*, *Kaninospirifer*, *Echinauris* and *Compressoproductus*, which, as noted above, have either restricted high palaeolatitudinal Boreal occurrences or low palaeolatitudinal Tethyan occurrences, the palaeogeographical distribution of *Spiriferella* is typically bipolar and bitemperate (terms as defined in Shi and Grunt, 2000), in that it occurred only in the middle and high palaeolatitudinal regions of both hemispheres (Shi and Grunt, 2000).

The mixed nature of the Xiujimqinqi brachiopod assemblage, as outlined above, is consistent with several other Middle Permian brachiopod faunas reported from northeast China, southeast Mongolia, South Primorye of the Russian Far East, and Japan, as already summarized and discussed by Tazawa (1991), Shi *et al.* (1995) and Shi and Zhan (1996). A refined scenario to interpret the origin of these mixed Middle Permian brachiopod faunas has recently been put forth by Shi and Tazawa (2001). In this interpretation, it is suggested that all the mixed Middle Permian







faunas in eastern Asia (NE China, parts of Japan, Mongolia, and South Primorye of the Russian Far East) are referable to characterize the same single palaeobiogeographical unit, the Sino-Mongolian-Japanese Province (= Inner Mongolia-Japanese Transitional Zone of Tazawa, 1991). This province has a distinct transitional biogeographical nature characterized by intermingling genera typical of both the palaeoequatorial Cathaysian Province in the south and the Boreal Realm to the north. The origin of this biogeographical mixing, apparently limited to the Wordian interval, is thought to have resulted from the interplay of three main factors: (1) a middle palaeolatitudinal position for the Sino-Mongolian-Japanese Province; (2) intensified plate convergence between the Sino-Korea and Mongolia blocks during the Permian; and (3) sea surface current connections with both the warm-water eastern Palaeo-Tethys to the south and the temperate to polar Arctic sea to the north (Figure 3). A middle palaeolatitudinal position for the Sino-Mongolian-Japanese Province, estimated to be 25°–40° N, is suggested by the mixed nature of the faunas which, in analogy to modern latitude-dependent biogeographical zonation patterns (see Yin, 1989), would indicate a mesothermal setting comparable to a middle-latitudinal position or temperate zone. A phase of intensified plate convergence between Sino-Korea and Mongolia through the Permian, especially the Early and Middle Permian is assumed because this would have resulted in the shrinking and progressive shallowing of the Sino-Mongolian seaway that harbored the Sino-Mongolian-Japanese Province. This in turn would have facilitated and enhanced the intermingling of Boreal faunas that originally prevailed on the shelves of the Mongolian block and the eastern Palaeo-Tethyan faunas that dominated the northern shelves of the Sino-Korea block. The inferred sea surface current connections of the Sino-Mongolian-Japanese Province to both the Boreal Realm and the eastern Palaeo-Tethys is important because these currents would have brought their prospective faunal elements to the Sino-Mongolian seaway where they were eventually intermingled. Therefore, in light of these considerations we propose that the Xiujimqinqi area was probably located within the eastern end of the Sino-Mongolian seaway, in an intermediate position between Sino-Korea and Mongolia

(Figure 3).

### Systematic palaeontology

Order Chonetida Nalivkin, 1979

Suborder Chonetidina Muir-Wood, 1955

Superfamily Chonetoidea Bronn, 1862

Family Rugosochonetidae Muir-Wood, 1962

Rugosochonetidae gen. and sp. indet.

Figure 4.1

*Remarks.*—An incomplete internal mould of a dorsal valve (NMV P308012) represents a species most likely of Rugosochonetidae in view of its prominent fold, finely papillose inner surface and about 20 coarse costellae each with scores of capillae. The specimen is badly worn, therefore the internal structures are not preserved, rendering even its generic status open.

Order Productida Waagen, 1883

Suborder Productidina Waagen, 1883

Superfamily Productoidea Gray, 1840

Family Productellidae Schuchert in Schuchert and LeVene, 1929

Subfamily Marginiferinae Stehli, 1954

Genus *Echinauris* Muir-Wood and Cooper, 1960

*Type species.*—*Echinauris lateralis* Muir-Wood and Cooper, 1960.

### *Echinauris* sp.

Figure 4.5

*Remarks.*—An incomplete ventral valve (NMV P308016) is referable to *Echinauris*. The ventral valve is more than 25 mm long, 29 mm wide, and more than 20 mm thick, has a moderately convex profile and is ornamented with numerous fine spine bases, but appears to have no evident internal ridge. This specimen is much larger than *E. jisuiensis* (Chao, 1927; also described and figured by Duan and Li, 1985, p. 112, pl. 35, figs. 7–13) from the Zhesi Formation in the Zhesi area of Inner Mongolia.

◀ **Figure 4.** 1. Rugosochonetidae gen. et sp. indet. Internal mold of a dorsal valve, NMV P308012,  $\times 2.5$ . 2–4, 6–8. *Anemonaria sublaevis* (King, 1931). 2. Ventral view of a ventral valve, NMV P308020,  $\times 2$ ; 3, 7. Posterior and anterior views of a ventral valve, NMV P308017,  $\times 2$ ; 4, 8. Ventral and lateral views of a ventral valve, NMV P308018,  $\times 2$ ; 6. Posterior view of a ventral valve, NMV P308019,  $\times 2$ . 5. *Echinauris* sp., ventral view of a ventral valve, NMV P308016,  $\times 1.3$ . 9. *Compressoproductus corniformis* (Chao, 1927), ventral view of a ventral valve, NMV P308026,  $\times 1.6$ . 10. *Cancrinella? cancrini* (de Verneuil, 1845), ventral view of a ventral valve, NMV P308024,  $\times 2$ . 11–14. *Spiriferella persaranae* (Grabau, 1931). 11–13. Lateral, dorsal, and ventral views of a conjoined shell, NMV P308029; 14. Ventral view of a ventral valve, NMV P308030,  $\times 1.5$ . 15, 18, 21. *Neospirifer* sp. Anterior, dorsal, and ventral views of a conjoined shell, NMV P308036. 16–17. *Spiriferella keilhavii* (von Buch, 1846). 16. Ventral view of a ventral valve, NMV P308033; 17. Ventral view of a ventral valve, NMV P308034. 19. *Neospiriferinae* gen. and sp. indet. Ventral view of a ventral valve, NMV P308037. 20. *Kaninospirifer* sp. Ventral view of a ventral valve, NMV P308035. All figures are natural size unless otherwise indicated.

Subfamily Paucispiniferinae Muir-Wood and Cooper, 1960  
Genus *Anemonaria* Cooper and Grant, 1969

*Type species.*—*Marginifera sublaevis* King, 1931.

*Anemonaria sublaevis* (King, 1931)

Figure 4.2–4.4, 4.6–4.8

*Marginifera sublaevis* King, 1931, p. 89, pl. 23, figs. 15a–c, ?16a, b, 19 (non figs. 13, 14).

*Anemonaria inflata* Cooper and Grant, 1969, p. 8, pl. 5, figs. 28, 29.

*Anemonaria sublaevis* (King). Cooper and Grant, 1975, p. 1103, pl. 408, figs. 1–26.

*Material.*—Three conjoined shells (NMV P308017–P308019) and a nearly complete ventral valve (NMV P308020).

*Description.*—Shell of medium size, subrectangular outline, strongly concavo-convex in profile; widest at hinge; anterior margin slightly emarginated medially; ears alate and acute, triangular in shape, well demarcated from visceral region. Ventral valve strongly but unevenly convex, strongly geniculated; umbonal region swollen; umbonal slopes sharply inclined; sulcus shallow and broad, originating from anterior to umbo, becoming prominent on trail. Dorsal valve deeply concave; fold broad and round on trail. Surface of both valves largely smooth; occasionally with some inconspicuous costae near margin; halteroid spines in row overhanging usually smooth ears; spines rare on body and trail.

*Remarks.*—King (1931) first named this species, but the type was selected by Cooper and Grant (1975). This species is characterized by subrectangular outline, broad and shallow sulcus, and small triangular ears. This species differs from *A. pseudohorrida* (Wiman, 1914, p. 74, pl. 17, figs. 1–11) from the Kungurian to Guadalupian Kapp Starostin Formation of Spitsbergen and *A. auriculata* Shi and Waterhouse (1996, p. 68, pl. 6, figs. 10–28; text-figs. 22–24) from the Artinskian Jungle Creek Formation in the Yukon Territory of Canada by its deeper and broader sulcus. *A. pinegensis* (Likharev, 1931, p. 26, pl. 3, figs. 24, 25; Sarytcheva, 1977, p. 123, pl. 18, figs. 5–14) from the Kungurian strata in Kanin Peninsula, northwestern Russia, could be conspecific with the present species in terms of its outline, and shallow and broad sulcus, but appears to have more subquadrate ears.

Superfamily Linoproductoidea Stehli, 1954

Family Linoproductidae Stehli, 1954

Subfamily Linoproductidae Stehli, 1954

Genus *Cancrinella* Fredericks, 1928

*Type species.*—*Productus cancrini* de Verneuil, 1845.

*Cancrinella? cancrini* (de Verneuil, 1845)

Figure 4.10

*Productus cancrini* de Verneuil, 1845, p. 273, pl. 16, figs. 8a–c; pl. 18, fig. 7; Likharev, 1931, p. 319, pl. 1, figs. 11–13; Miloradovich, 1935, p. 131, pl. 5, figs. 4, 5.

*Cancrinella cancrini* (de Verneuil). Sarytcheva and Sokolskaja, 1952, p. 112, pl. 20; Grigorjeva, 1962, p. 50, pl. 11, figs. 1–10; pl. 15, fig. 1; pl. 16, figs. 1, 2; Grigorjeva *et al.*, 1977, p. 129, pl. 19, figs. 1–9, text-figs. 75, 76.

*Material.*—A complete ventral valve (NMV P308024) and an incomplete external mould of a dorsal valve (NMV P308025).

*Description.*—Shell small, subquadrate in outline, hinge slightly narrower than greatest width; with broadly rounded anterior and lateral margins; ventral visceral disc strongly convex, somewhat triangular; beak pointed; ears small; cardinal extremities obtuse; umbonal slopes sharply inclined; sulcus absent; surface marked by strong concentric wrinkles and fine costellae; costellae numbering 7 in 2 mm near the anterior margin; spines thin and delicate; spine bases elongated, widely scattered. Dorsal valve deeply concave; strongly geniculated; surface also with distinct wrinkles and fine costellae; spines unknown.

*Remarks.*—The small size, subquadrate outline and very fine costellae of the present specimens are generally identical with the type figured by de Verneuil (1845). However, the unknown dorsal spines renders the generic status of the present material open. Many previously recognized species of *Cancrinella* have been attributed to *Costatumulus* Waterhouse (see Archbold, 1993), which differs from *Cancrinella* in possessing dorsal spines. Therefore, it is also possible that the Xiujinqin specimens could belong to *Costatumulus*.

Genus *Compressoproductus* Sarytcheva in Sarytcheva, Likharev and Sokolskaja, 1960

*Type species.*—*Productus compressus* Waagen, 1884.

*Compressoproductus corniformis* (Chao, 1927)

Figure 4.9

*Striatifera compressa* var. *corniformis* Chao, 1927, p. 101, pl. 15, figs. 6–9.

*Productus (Stratifera)* var. *corniformis* Chao. Grabau, 1931, p. 291, pl. 29, figs. 6–9.

*Compressoproductus compressa* var. *corniformis* (Chao). Wang *et al.*, 1964, p. 334, pl. 53, figs. 12, 13.



*Remarks.*—The occurrence of this species in the Xiujimqinqi collection is shown by a single specimen (NMV P308026). This species has been documented from the Zhesi Formation in Zhesi, Inner Mongolia, by Grabau (1931). The characteristic elongate outline, finely costellate surface and strongly laterally compressed nature of the shell of the present specimen fit very well with the type from the Longtan Formation in Guangxi, South China, as figured by Chao (1927). This species differs from all other species in the genus by the laterally compressed nature of its shell, hence warranting the recognition of Chao's variety as a separate species.

Order Spiriferida Waagen, 1883  
Suborder Spiriferidina Waagen, 1883  
Superfamily Spiriferoidea King, 1846  
Family Spiriferellidae Waterhouse, 1968  
Genus *Spiriferella* Tschernyschew, 1902

*Type species.*—*Spirifer saranae* de Verneuil, 1845.

*Spiriferella persaranae* (Grabau, 1931)

Figure 4.11–4.14

*Spirifer persaranae* Grabau, 1931, p. 156, pl. 19, fig. 4.  
*Spiriferella persaranae* Grabau. Wang *et al.*, 1964, p. 595, pl. 114, figs. 15, 16; Li and Gu, 1976, p. 295, pl. 172, figs. 1–6; Li *et al.*, 1980, p. 418, pl. 178, fig. 5; Duan and Li, 1985, p. 121, pl. 1, figs. 1–11, 17, 18.

*Material.*—A slightly crushed conjoined shell (NMV P308029) and three incomplete ventral valves (NMV P308030–308032).

*Description.*—Shell medium in size, elongate in outline, unequally biconvex in profile, hinge narrower than greatest width at slightly anterior to midvalve; ventral beak strongly incurved; interarea very high, strongly concave, delthyrium about one-third of the hinge line; beak ridges angular; ventral sulcus narrow and shallow, commencing from beak, with several inconspicuous costae; boundary costae coarser than other costae; each flank with 4–6 costae; costae commonly bifurcating 1–2 times, producing some small costae beside the main costa; dorsal valve less convex than ventral valve; fold low, with a prominent median groove; each flank with 4–5 costae.

*Remarks.*—*S. saranae* (de Verneuil, 1845, p. 169, pl. 6, fig. 15a, b) is closest to this species. The original description of *S. saranae* by de Verneuil (1845) from the upper Artinskian of the Ufa River mentioned that this species is characterized by a high interarea, five to six smaller, equally spaced costae in the sulcus and a prominent median groove in the fold. *S. persaranae* differs from *S. saranae* in its more simple costae and less conspicuous and proba-

bly fewer and smaller costae in the sulcus. *S. praesaranae* (Stepanov, 1948, p. 43, pl. 10, figs. 3–8) is probably synonymous with the present species as indicated by their similar costation, size and outline, but it is from the Upper Carboniferous.

*Spiriferella keilhavii* (von Buch, 1846)

Figure 4.16, 4.17

*Spirifer keilhavii* von Buch, 1846, p. 74, pl. 1, figs. 2a, b; Frech, 1901, p. 499, pl. 57c, figs. 1b–c.  
*Spirifer draschei* Toulou, 1875, p. 239, pl. 7, figs. 4a–c.  
*Spirifer parryanus* Toulou, 1875, p. 232, pl. 7, figs. 8a–d.  
*Spiriferella keilhavii* (von Buch). Tschernyschew, 1902, p. 527, pl. 40, figs. 1–4; Wiman, 1914, p. 36, pl. 2, figs. 25–30, pl. 3, fig. 1; Tschernyschew and Stepanov, 1916, p. 79, pl. 11, figs. 2a–c, 3a–c; Frebold, 1931, p. 28, pl. 5, figs. 7–9; 1937, p. 46, pl. 11, fig. 9; Dunbar, 1955, p. 139, pl. 25, figs. 1–9; pl. 26, figs. 1–11; pl. 27, figs. 1–14; Gobbett, 1964, p. 154, pl. 20, fig. 7; Nelson and Johnson, 1968, p. 736, pl. 96, figs. 7, 8, 12; text-figs. 3e, 8a, 9, 13b; Brabb and Grant, 1971, p. 17, pl. 2, figs. 26–28, 34, 35; Duan and Li, 1985, p. 122, pl. 2, figs. 1, 5, 8.  
*Spiriferella draschei* (Toulou). Wiman (partim), 1914, p. 38, pl. 3, fig. 2.  
? *Spiriferella keilhavii* (von Buch). Waterhouse and Waddington, 1982, p. 28, pl. 4, fig. 15; pl. 6, figs. 3–14; text-figs. 16e, g–i, 19.

*Remarks.*—As noted by Likharev and Einor (1939, p. 218) and Dunbar (1955, p. 152), von Buch's original figure of *S. keilhavii* is a drawing constructed from a number of specimens, two of which (a dorsal and a ventral) were later figured by Frech (1901, pl. 57c, figs. 1b–c). Likharev and Einor (1939) selected the dorsal valve of Frech's figured material (Frech, 1901, pl. 57c, fig. 1b) as the 'holotype' (lectotype) of *S. keilhavii* on the ground that the features of the dorsal valve match better with von Buch's original description of the species. Since our material consists only of two ventral valves (NMV P308033, 308034), no comparison can be made with the lectotype of the species, but the observed features of the ventral valves, especially the large and wide valves with a hinge line nearly as wide as the greatest shell width and strongly fasciculated costae, are characteristic of the ventral valve of *S. keilhavii* as figured by Tschernyschew (1902), Dunbar (1955) and Gobbett (1963).

*Spirifer parryanus* Toulou (1875) from Spitzbergen was erected based on several incomplete specimens, and has been referred to *S. keilhavii* (Dunbar, 1955, p. 145). Specimens figured by Waterhouse and Waddington (1982) from Yukon Territory of Canada have flat, coarse and unbranched costae and a relatively narrower hinge, suggest-

ing that they are probably different from the type material of *S. keilhavii* as described and figured by Dunbar (1955, pl. 27, figs. 8, 9).

Family Spiriferidae King, 1846  
Subfamily Kaninospiriferinae Kalashnikov, 1996  
Genus *Kaninospirifer* Kulikov and Stepanov  
in Stepanov *et al.*, 1975

*Types species.*—*Spirifer kaninensis* Likharev, 1943.

*Remarks.*—When proposing Kaninospiriferinae, Kalashnikov (1996) included two genera in this new subfamily: *Kaninospirifer* and *Imperiospira* Archbold and Thomas, 1994. The former is distinguished from the latter by its transverse outline, ill-defined fasciculation if present at all, and lack of adminicula within the ventral interior. On the other hand, both genera are readily distinguished from members of the Neospiriferinae by fine and equidimensional costae, generally weak fasciculation and absent to weakly developed adminicula.

As already noted, *Kaninospirifer* has very limited stratigraphical and geographical distributions. Kalashnikov (1996) has listed the genus occurring mainly in the Arctic region (Arctic Canada, Greenland, Spitsbergen, Arctic Russia) and East Asia (South Primorye of Far East of Russia, southeast Mongolia, northeast China). Pavlova (1991, p. 130) also listed some previously reported species from Timor and the Salt Range as possible representatives of the genus, but the true identities of these species have not yet been confirmed. On the other hand, *Gypospirifer* sp. from the Middle Permian of the Hida Gaien Belt of central Japan (Tazawa, 2000, figs. 3.12, 3.13) appears referable to *Kaninospirifer* judging by its shape and costation pattern. In all of its confirmed occurrences, *Kaninospirifer* is known to be associated with Kazanian (or Wordian) faunas.

*Kaninospirifer* sp.

Figure 4.20

*Remarks.*—An incomplete ventral valve (NMV P308035) in the collection indicates *Kaninospirifer*. The specimen is characterized by a transverse outline, very weak fasciculation that is visible only on the umbo, fine and equidimensional costae numbering about 15 per cm at about 2 cm from the beak, and a broad and well defined sulcus. This specimen appears to be closest to *Kaninospirifer kaninensis* (Likharev, 1943, p. 279, figs. 1–4), type species of the genus, from the Kazanian (Wordian) of the Kanin Peninsula, Russia. The two forms share a transverse outline, weak fasciculations that do not form prominent bundles, fine and even costae, and a well developed sulcus, but further comparison is hampered because of insufficient material in our collection, especially

the total lack of knowledge of the interior.

Pavlova (1991) assigned several species from the Middle Permian of Mongolia, South Primorye of Russian Far East, and northeast China to *Kaninospirifer*. Both *K. incertiplicatus* Pavlova (1991, p. 131, pl. 29, figs 5, 6; see also Fredericks, 1925, p. 27, pl. 4, figs. 111, 112) and *K. adpressum* (Liu and Waterhouse, 1985, p. 36, pl. 12, figs. 5–10; see also Pavlova, 1991, p. 132, pl. 29, figs. 7, 8) are larger than the present specimen, less transverse and more subquadrate in outline, and possess variably developed plicae on the shell surfaces.

*Gypospirifer* sp., from the Middle Permian Moribu Formation of the Hida Gaien Belt of central Japan (Tazawa, 2000, figs. 3.12, 3.13), is likely a representative of *Kaninospirifer*, judging by its transverse outline, relatively fine and even costae and ill-defined fasciculation, but the ventral valve (Tazawa, 2000, fig. 3.12) seems to display slightly coarser costae than the present specimen.

Subfamily Neospiriferinae Waterhouse 1968  
Genus *Neospirifer* Fredericks 1923

*Type species.*—*Spirifer fasciger* von Keyserling, 1846.

*Neospirifer* sp.

Figure 4.15, 4.18, 4.21

*Remarks.*—An incomplete conjoined shell (NMV P308036) has a deeply V-shaped sulcus in the ventral valve and a highly elevated fold in the dorsal valve. The crests of the plicae that bound the sulcus are sharp. Costae on flanks are fascicostellate and fine, numbering about 10 per cm near the anterior margin. Each fascicle consists of 6–8 costae. This species differs from any known species of *Neospirifer* by its fine costae on both valves and the deep, V-shaped sulcus. *N. fasciger* (von Keyserling, 1846) is somewhat similar to this species in terms of its outline and general fasciculation pattern, but differs by its shallower and U-shaped sulcus and coarser costae.

Neospiriferinae gen. and sp. indet.

Figure 4.19

*Remarks.*—An incomplete ventral valve (NMV P308037) indicates possibly another species of *Neospirifer* or a related genus. The specimen has a subquadrate outline, weak fasciculation, coarse and somewhat flattened costae which are grouped into bundles of two to four (generally three), and a relatively broad and shallow sulcus. No known species of *Neospirifer* seems to resemble this specimen very closely. On the other hand, *Cratispirifer nuraensis* Archbold and Thomas (1985, p. 280, figs. 8A–F)



from the Sakmarian of Western Australia appears comparable in general terms, especially on account of their coarse, flattened and equidimensional costae that are grouped into bundles of no more than four (usually three), but the latter species is clearly distinguishable by its transverse outline, a proportionally high ventral interarea, and flattened costae. *Spirifer*? sp. from the Kungurian Talatinsk Formation of the Kozhim River section of the Pechora Basin, Russia (Kalashnikov, 1998), shares a similar outline and costation pattern with the present specimen, but it has a deeper sulcus and a more convex umbonal region.

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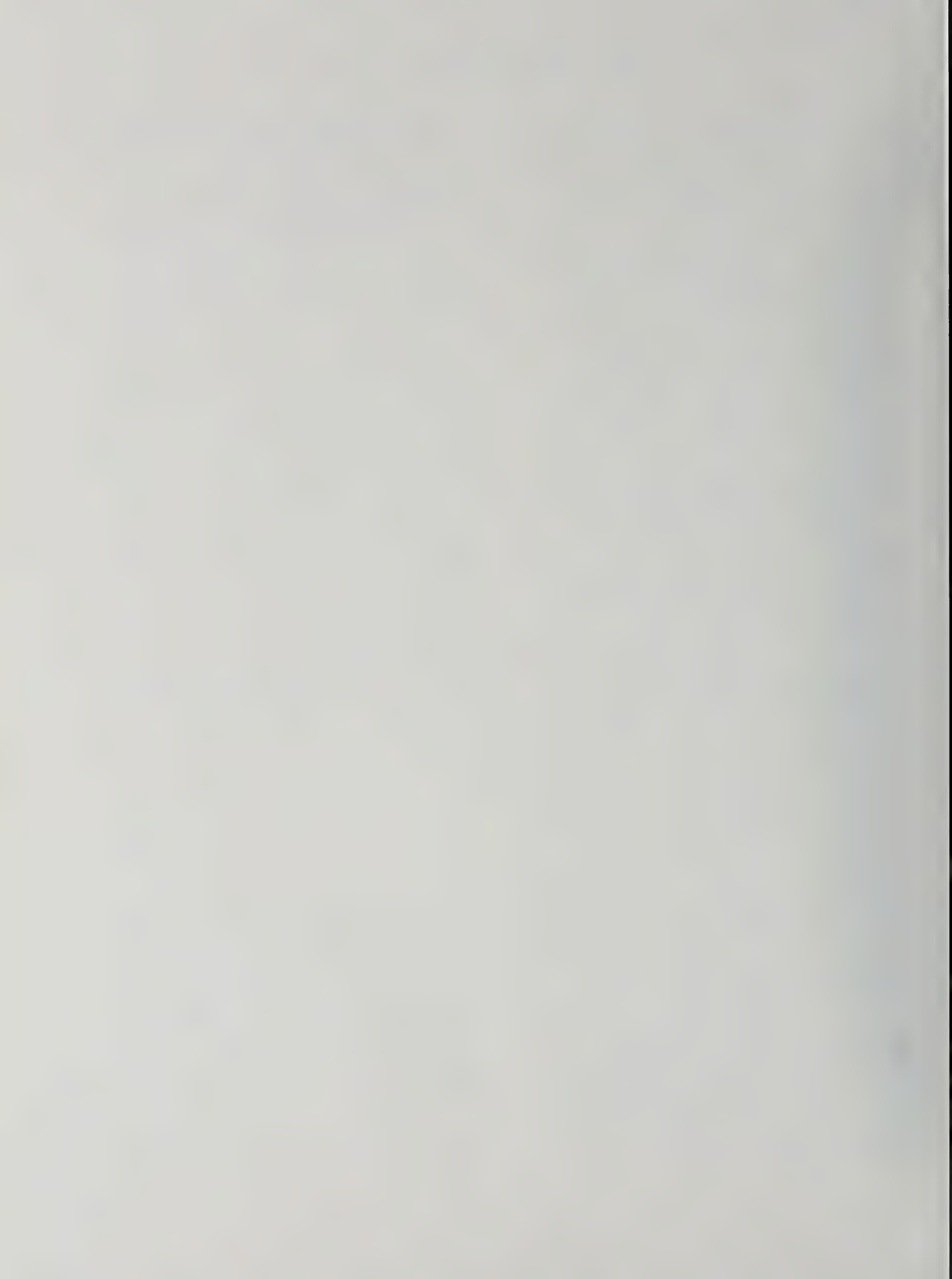
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# The Recent rhynchonellide brachiopod *Parasphenarina cavernicola* gen. et sp. nov. from the submarine caves of Okinawa, Japan

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**Abstract.** A new micromorphic rhynchonellide brachiopod *Parasphenarina cavernicola* gen. et sp. nov. is described from submarine caves on the outer slopes of coral reefs in the Ryukyu Islands, Japan. Based on the presence of spinuliform crura, the new genus is included in the Family Frieleiidae Cooper, the diagnosis of which is emended. Detailed morphological observations of different-sized shells and intraspecific variability have shown that the morphology of the hinge plates changes considerably during ontogeny. It is suggested that the new genus *Parasphenarina* could have evolved from forms close to the extremely rare bathyal Pliocene genus *Sphenarina* Cooper. The diagnostic characteristics of *Parasphenarina* such as diminutive adult size and lack of septalium and median septum may represent paedomorphic evolution.

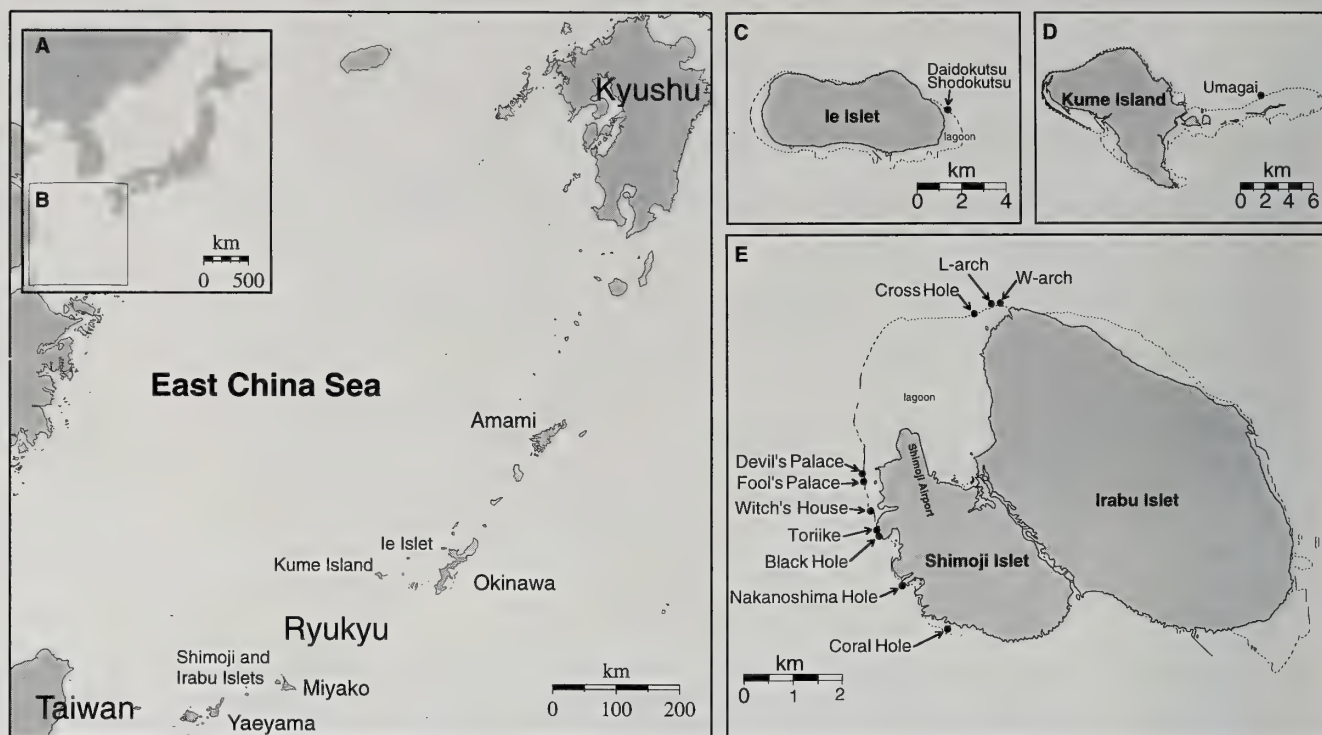
**Key words:** Brachiopoda, Japan, Okinawa, ontogenetic variability, paedomorphic process, *Parasphenarina cavernicola* gen. et sp. nov., Recent, submarine cave

## Introduction

Studies on the benthic fauna from more than thirty submarine caves on the outer slopes of coral reefs in the Ryukyu Islands and adjacent areas have been conducted since 1989. Thanks to the SCUBA diving technique it was possible to explore in detail the caves and collect a large amount of sediment samples. The samples turned out to be rich in many interesting organisms characteristic of cryptic habitats, such as bivalves, gastropods, chitons, polychaetes, crustaceans, brachiopods, bryozoans, echinoids, ahermatypic corals, sponges and benthic foraminifers. A number of taxonomic studies have been subsequently published: on molluscs (Hayami and Kase, 1992, 1993, 1996; Kase and Hayami, 1992; Kase and Kinjo, 1996) and ostracodes (Tabuki and Hanai, 1999). They report many unusual characteristics of the fauna, such as reduced adult size, anachronistic shell forms and life styles, paedomorphic forms in comparison with supposed ancestors, and unique taxonomic assemblages including many typical bathyal and abyssal genera. Some apparent

'living fossils' inhabiting the sheltered environment of the submarine caves were also discovered. The fauna as a whole is almost entirely different from that found in adjacent seas outside the caves.

The brachiopods collected from the submarine caves of the Ryukyu Islands include several species as yet undescribed. Among the brachiopod assemblage, a single rhynchonellide species was found. This paper describes this new, micromorphic, thin, transparent-shelled rhynchonellide species. Initially the new species was assigned with a query to the Pliocene genus *Sphenarina* Cooper, 1959 (Saito *et al.*, 2000). Based on detailed morphological observations, study of the ontogeny, and comparison with the type species of the genus *Sphenarina*, we found enough evidence to propose a new genus for the rhynchonellides from the Okinawa submarine caves, herein named *Parasphenarina cavernicola* gen. et sp. nov. The closest taxon to the new species is *Sphenarina ezogremena* Zvezina (Zvezina, 1981) known from a single specimen from the Flores Sea. We include the species *S. ezogremena* in the new genus *Parasphenarina*. The new genus could



**Figure 1.** Locality maps (after Hayami and Kase, 1993). **A.** Index map. **B.** Detail of **A** showing Ie, Irabu and Shimoji Islands. **C.** Localities of submarine caves of Ie Islet. **D.** Localities of submarine cave of Kume Island. **E.** Submarine caves of Shimoji Islet and Irabu Islet in Miyako Islands.

have evolved from forms morphologically close to the extremely rare bathyal Pliocene genus *Sphenarina* from Sicily (cf. Cooper, 1959; Gaetani and Saccà, 1984). It is suggested that the diagnostic characteristics of *Parasphenarina* such as diminutive adult size and lack of septalium and median septum may have resulted from paedomorphic evolution.

#### Study area and methods of investigation

The submarine caves of Okinawa vary in size and topography, although they have many common characteristics. The caves are open to the forereef slopes, and their morphology is complicated, winding and bifurcating, with numerous crevices. The caves are in the Pleistocene Ryukyu Limestone, and generally have entrances at about 15 to 40 m water depth and horizontal lengths ranging from several meters to more than 70 m. Sediments on the cave floors are composed of calcareous mud and bioclasts. They are almost free of coarse terrigenous material (Hayami and Kase, 1996). The caves were probably formed by ground water during some lower sea level stages in the Pleistocene and finally drowned during the postglacial rise of sea level (Kase and Hayami, 1992; Hayami and Kase, 1993, 1996). Twelve submarine caves of the Ryukyu Islands (one is lo-

cated in Kume Island, two in Ie Islet, seven in Shimoji Islet, and two in Irabu Islet, Miyako Islands (Figure 1) yielded specimens of *Parasphenarina cavernicola* for this study. Sessile benthic biota were collected by brushing the surfaces of walls, ceilings and undersides of boulders or large shells of dead bivalves such as *Pycnodonte taniguchii*, with the assistance of divers. Boulders and dead bivalves that could be brought to the surface, as well as sediments in the caves, were also collected to look for live and dead individuals under the binocular microscope. The morphology of the specimens was examined both under the binocular and scanning electron microscopes (SEM). For observing the microstructure of the primary layer surface, selected shells of *Parasphenarina cavernicola* were treated with domestic-grade bleach (sodium hypochlorite: approximately 5% (v/w)) for 12 to 18 hours to remove surface debris and the periostracum, then washed, dried, and mounted on stubs for SEM. Other shells were dried and embedded in epoxy resin, transversely cut at the maximum shell width, polished with a set of diamond powders and subsequently etched with 5% (v/v) HCl for 5 seconds. Other specimens after drying were broken to observe the uneven natural fracture of the primary calcitic layer. All samples were then coated with Pt-Pd alloy, and photographed by a Hitachi S-2400S scanning electron microscope. The





Figure 2. Holotype of *Parasphenarina cavernicola* gen. et sp. nov., Umut RB28220-MN01-a, 'Nakanoshima Hole', Shimoji Islet, Miyako Island.

measurements of *Parasphenarina cavernicola* were taken using the Nikon profile projector V-12BDC.

The specimens of *Sphenarina sicula* Davidson from the Pliocene of Messina, (Sicily, Italy), borrowed for comparison from the Smithsonian Institution, National Museum of Natural History (USNM 549381a, b; Cooper, 1959), were photographed with a Hitachi S-2250N natural SEM without coating. One of the borrowed specimens (USNM 549381b) was embedded in epoxy and transversely sectioned to compare with the sections of the new species *P. cavernicola*.

### Systematic description

Class Rhynchonellata Williams *et al.*, 1996

Order Rhynchonellida Kuhn, 1949

Family Frieleiidae Cooper, 1959

**Emended diagnosis.**—Capillate to costellate or smooth rhynchonellides with subtriangular to teardrop outline and spinuliform crura.

**Remarks.**—The family Frieleiidae was created by Cooper (1959) for capillate to costellate rhynchonellide genera with triangular outline, strong dental plates and spinuliform crura, supported by short plates uniting with the septum of the dorsal valve to form a septalium. At the same time Cooper (1959) introduced the family Hispanirhynchiidae for rhynchonellides having spinuliform crura, low or no median ridge but no septalium in the dorsal valve. In the first edition of the brachiopod volumes of the Treatise on Invertebrate Paleontology (Ager, 1965) the hispanirhynchiids were included in the family Frieleiidae,

even though the hispanirhynchiid genera *Hispanirhynchia* Thomson and *Sphenarina* Cooper do not possess or have only a low median ridge in the dorsal valve and do not have a septalium by original diagnosis. However, according to our new observations (see below) on the type material of *Sphenarina*, this genus does possess an incipient septalium in the adult dorsal valve. This feature brings *Sphenarina* closer to the frieleiid genera with a septalium. Thus the separation of the hispanirhynchiid species into a family or subfamily seems not to be justifiable now, until a reappraisal of other genera like *Hispanirhynchia*, *Manithyris* Foster and *Abyssorhynchia* Zezina demonstrates the lack of a septalium in the adult forms. The new genus *Parasphenarina* lacks a septalium and a typical median septum. In the present state of knowledge we prefer to emend the diagnosis of the family Frieleiidae to exclude the presence of a septalium from the diagnosis and to include smooth-shelled genera like *Parasphenarina* into the family. Frieleiidae ranges from Pliocene to Recent.

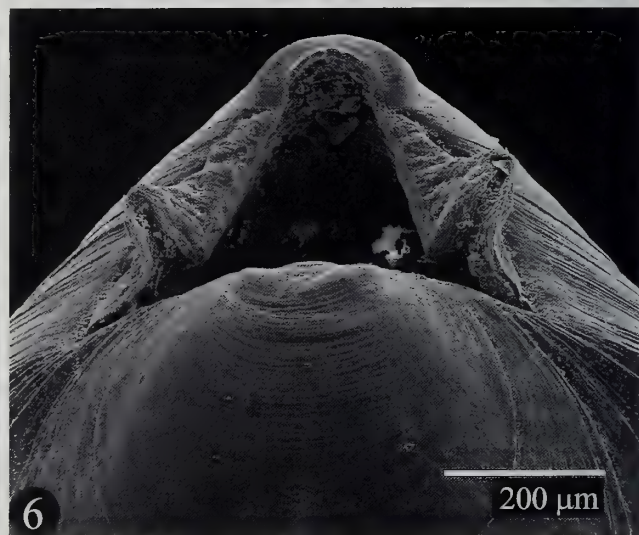
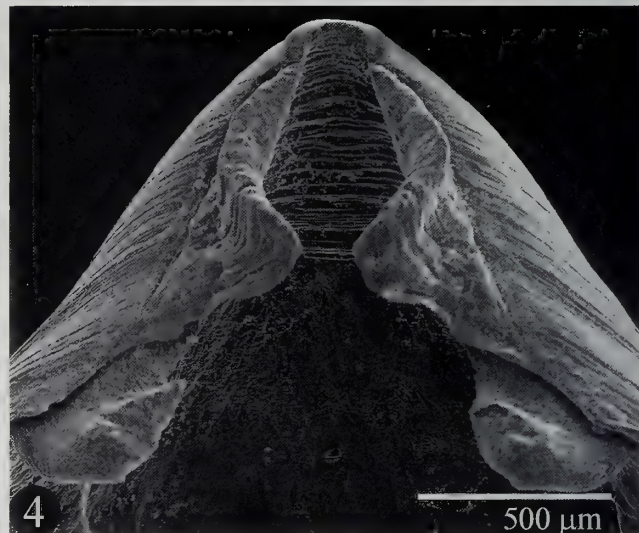
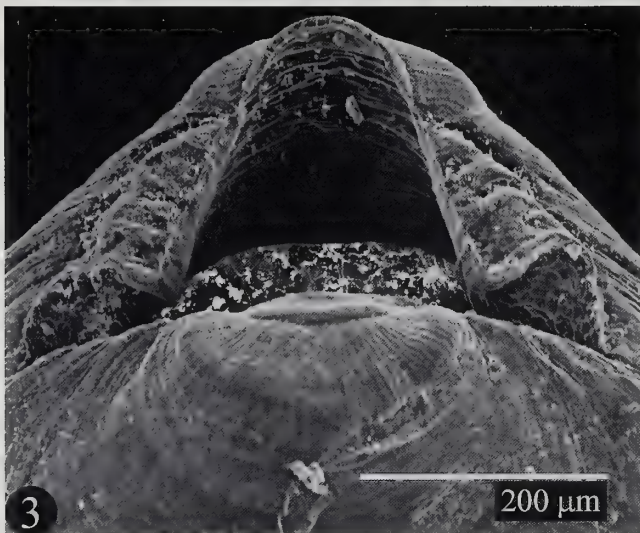
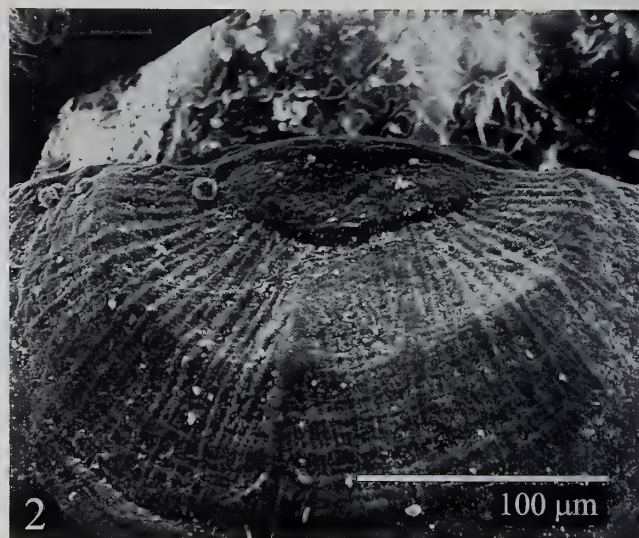
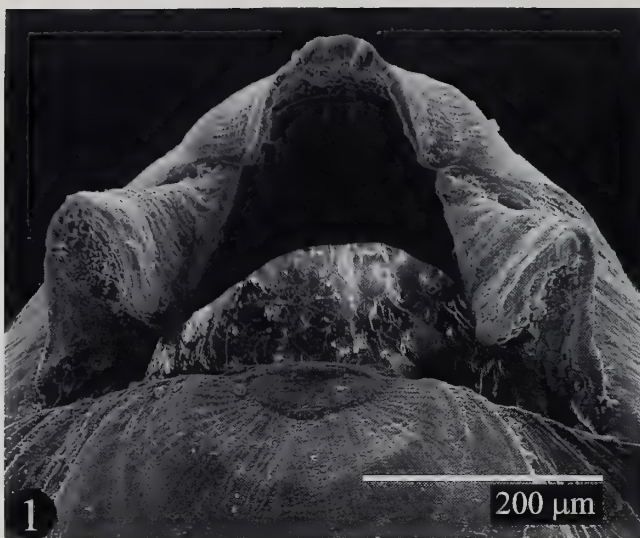
### Genus *Parasphenarina* gen. nov.

**Type species.**—*Parasphenarina cavernicola* sp. nov., Recent, Okinawa Islands, Japan.

**Derivation of name.**—From Greek *para* = near, close to, referring to the similarity to the genus *Sphenarina* and suggesting that *Parasphenarina* could have evolved from forms close to *Sphenarina*.

**Diagnosis.**—Diminutive smooth teardrop-shaped to triangularly oval rhynchonellides with smooth semitransparent shell; subequivalve, rectimarginate anterior commissure; suberect to straight beak, hypothyrid auriculate







foramen, disjunct deltidial plates. Dorsal valve lacks a median ridge, though a shallow groove between two low ridges may be present instead. Crura spinuliform; cardinal process and septalium absent. Hinge plates and inner socket ridges do not meet together in posterior part of dorsal valve.

*Species assigned.*—Besides the type species *Parasphenarina cavernicola* sp. nov., only one more species based on a single specimen and referred previously to the genus *Sphenarina*, is here included in the new genus—the Recent *Sphenarina ezogremena* Zezina, found in the Flores Sea, north of Bali Island. Thus, the new combination *Parasphenarina ezogremena* (Zezina) is adopted below.

*Remarks.*—*Parasphenarina* is most similar to the genus *Sphenarina* Cooper, 1959 from the Pliocene of Sicily, Italy. Initially we tentatively assigned the new cave rhynchonellid species to the genus *Sphenarina* (Saito *et al.*, 2000) based on similar shape, spinuliform crura, rectimarginate anterior commissure, well developed hinge plates and lack of a median septum and septalium. According to the original diagnosis, *Sphenarina* does not possess a median septum. We examined the type material of *Sphenarina* used by Cooper, deposited at the National Museum of Natural History, Smithsonian Institution, Washington. Additionally we borrowed for comparison and serially sectioned one of the topotype specimens from the Pliocene of Messina (Sicily, Italy). In contrast to Cooper's diagnosis (1959, p. 63) we discovered a low median septum and a small incipient septalium in the umbonal part of the dorsal valve of the sectioned specimen of *Sphenarina sicula* (Davidson). The sectioned specimen with septalium (Figure 14.2) was larger (L = 15.60 mm, W = 15.10 mm, T = 8.40 mm) than the one figured by Cooper (1959, Pl. 8–A7) and in this paper on Figure 14.1 (L = 12.55 mm, W = 10.50 mm, T = 6.60 mm). It is possible that the septalium in *Sphenarina* develops in the late adult stage only and is not present in juvenile individuals. Since *Sphenarina* is an extremely rare genus (Gaetani and Saccà, 1984; personal communication, 2001) it is not possible to section further material to check the development of a septalium in other adult shells. However, a similar example of presence of a better developed septalium in a large specimen of *Burmishynchia turgida* Buckman from the Bathonian of Laz, Yugoslavia is figured by Radulović (1991, figs 4, 5). From our data, we can assert that the new genus *Parasphenarina* differs from the Pliocene genus *Sphenarina* in the lack of a median septum and septalium in the adult stage. The hinge plates and the inner socket

ridges of the new genus do not meet at the top of the dorsal valve, and remain separated (Figures 5.1, 5.3, 5.5, 6.3). In contrast, the hinge plates and the inner socket ridges of *Sphenarina* meet together at the top of the dorsal valve. Additionally, an incipient cardinal process was noted in the specimen dissected by Cooper (Figure 14.1). *Parasphenarina* is micromorphic in size and has completely smooth shells, disjunct auriculate deltidial plates, poorly developed dental plates, delimiting narrow umbonal cavities and an elaborate pedicle collar, while *Sphenarina* is larger in size, finely capillate, with deltidial plates that can be conjunct (towards later ontogenetic stages), and has well developed dental plates and a shorter pedicle collar. The revision of the genus *Sphenarina* will be discussed elsewhere.

*Parasphenarina* is externally similar to *Cryptopora* Jeffreys and *Tethyrhynchia* Logan. However the three genera can be easily distinguished by their internal morphology, especially by the development of three different types of crura: spinuliform, maniculiform and luniform respectively, which places them in three different families.

*Parasphenarina cavernicola* sp. nov.

Figures 2–12

*Sphenarina?* sp., Saito *et al.*, 2000, p. 77; Saito *et al.*, 2001, p. 131, 132.

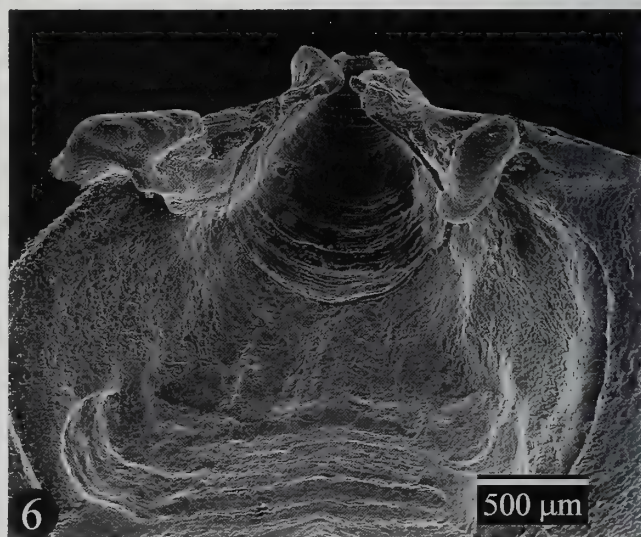
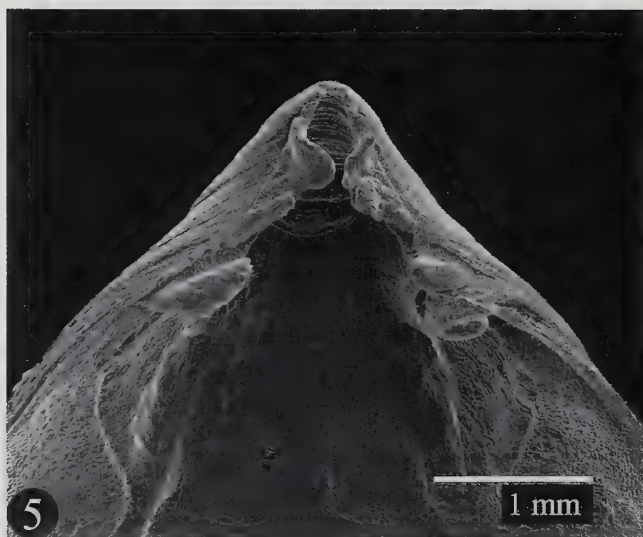
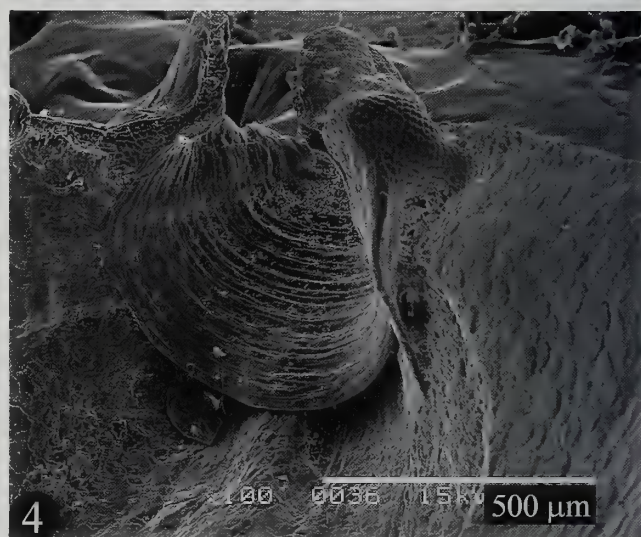
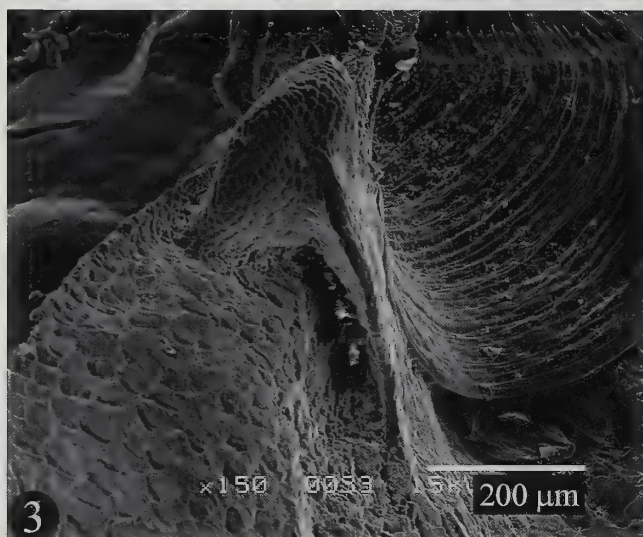
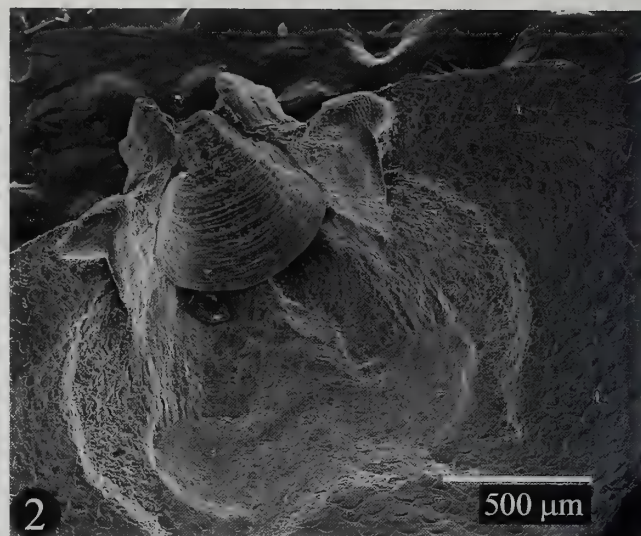
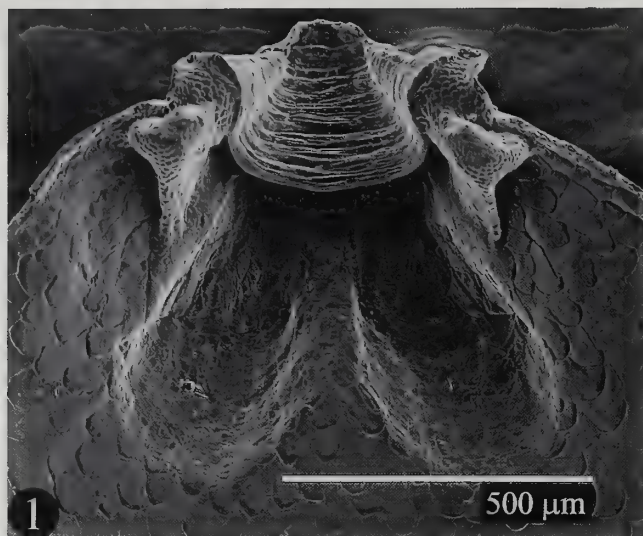
*Derivation of name.*—From Latin *caverna* = cave plus the Latin suffix *-cola* = dweller, inhabitant, after its occurrence in submarine caves.

*Holotype.*—The holotype specimen (UMUT RB28220-MN01-a) (Figure 2) and 19 paratypes (UMUT RB28220-MN01-b) were collected at 27 m depth from the bottom of the cave 'Nakanoshima Hole', Shimoji Islet, Miyako Island. The holotype and all the paratypes are deposited at the University Museum, the University of Tokyo (UMUT).

*Material and occurrence.*—Twenty-one living specimens and more than 80 intact dead shells, many separated valves and fragments from 12 submarine caves in coral reefs of the Ryukyu Islands (Figure 1). The material is deposited at the University Museum, the University of Tokyo (UMUT RB28210–28222). One complete specimen, two ventral and two dorsal valves are housed at the National Museum of Natural History, Sofia (NMNHS 31068). Brief descriptions, the location of the caves and sample numbers are given below. The appended data on the geographical position, length, bottom depth and description of these caves are from Hayami and Kase (1993) with two ad-

◀ **Figure 3.** *Parasphenarina cavernicola* gen. et sp. nov., Shimoji Islet, Miyako Island. 1. Umbonal part of specimen UMUT RB28220-R1-7, 'Nakanoshima hole'. 2. Detail of 1 showing the fine capillation anterior to the protegular node. 3. Umbonal part of specimen UMUT RB28220-R1-6, 'Nakanoshima hole'. 4. Ventral beak showing the teeth and disjunct deltidial plates UMUT RB28220 R5 8, 'Nakanoshima hole'. 5. Subcircular juvenile specimen UMUT RB28219-R4-1, 'Coral hole'. 6. Detail of 5 showing the umbonal part.







ditional caves ('Umagai' and 'Nakanoshima Hole') not mentioned by them. The bottom depth data are given for the entrances and the innermost parts of the caves: **Kume Island:** 1. 'Umagai' cave (26° 21.3' N, 126° 53.3' E), more than 25 m long, curved tunnel, innermost part is totally dark (-28.3 m to 26 m deep), UMUT RB28210-KU05. **Ie Island:** 2. 'Shodokutsu' (26° 42.9' N, 127° 50.1' E), more than 30 m long, totally dark, winding and branching tunnel (-20 to -7 m deep), UMUT RB28211-IS01, IS 02, IS05, IS23; 3. 'Daidokutsu' (26° 42.9' N, 127° 50.1' E), about 10 m long, very dark, cathedral-like wide cave (-20 m deep), UMUT RB28212-ID07, ID11, ID14, ID17, ID18; a mixed sample UMUT RB28213-ISD01 from 'Shodokutsu' and 'Daidokutsu' caves. **Shimoji Island.** 4. 'Devil's Palace' (24° 49.6' N, 125° 08.2' E), about 15 m long, dark tunnel (-25 m deep) with some narrow openings on the ceiling, UMUT RB28214-MD02, MD03; 5. 'Fool's Palace' (24° 49.6' N, 125° 08.2' E), about 10 m long, almost totally dark tunnel (-35 to -32 m deep), #UMUT RB28215-MF01, MF02, MF04, MF05; 6. 'Witch's House' (24° 49.3' N, 125° 08.3' E), more than 10 m long, totally dark tunnel (-37 to -35 m deep), UMUT RB28216-MM06, MM07, MM09; 7. 'Toriike' (24° 49.1' N, 125° 08.3' E), a famous diving point, about 30 m long, large dark tunnel connected with two large side tunnels (-40 to -12 m deep), UMUT RB28217-MT06; 8. 'Black Hole' (24° 49.1' N, 125° 08.3' E), about 70 m long, totally dark stepwise tunnel with an air pocket in the innermost part (-35 to 0 m deep), UMUT RB28218-MB06; 9. 'Coral Hole' (24° 48.0' N, 125° 09.0' E), about 5 m long, dark hole and tunnel (-35 m deep), UMUT RB28219-MS01, MS02, MS03, MS05, MS06, MS07, MS08, MS09, MS10, MS12, MS13, MS16, MS17; 10. 'Nakanoshima Hole' (24° 48.47' N, 125° 08.65' E), a submarine cave totally dark inside, entrance about 20 m deep, UMUT RB28220-MN01 (including the holotype and paratype), MN02, MN03. **Irabu Island.** 11. 'W-arch' (24° 51.7' N, 125° 09.7' E), double dark caves with an opening on the ceiling (-15 to -13 m deep), UMUT RB28221-MW01, MW05; 12. 'Cross Hole' (24° 51.67' N, 125° 09.5' E), 20 m long, dark hole with complicated morphology (-25 to -20 m deep), UMUT RB28222-MC13.

**Ecology and associated brachiopods.**—Live individuals of *Parasphenarina cavernicola* were mainly found attached to the undersides of hard substrates lying on the cave floor near the entrance, and were occasionally found on the cave wall at the middle of dark tunnels (such as 'Coral Hole') as

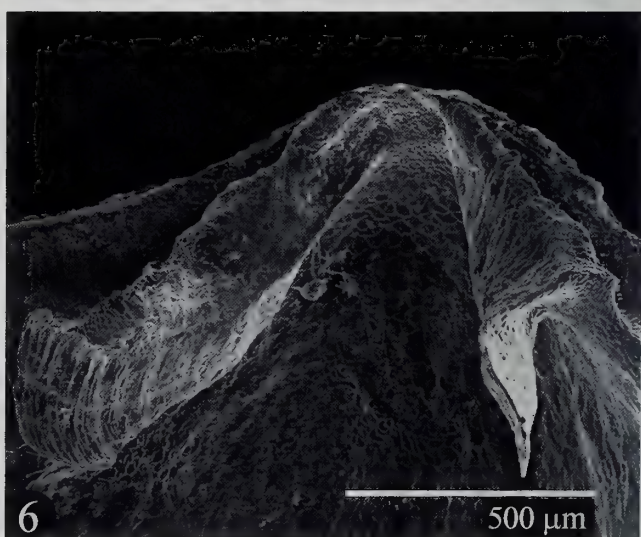
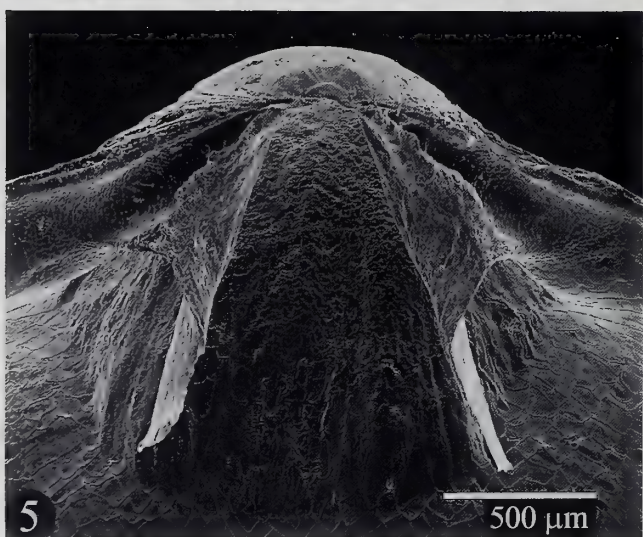
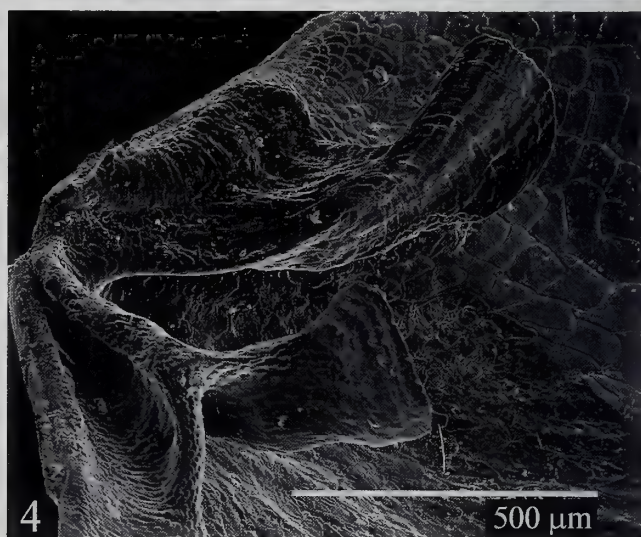
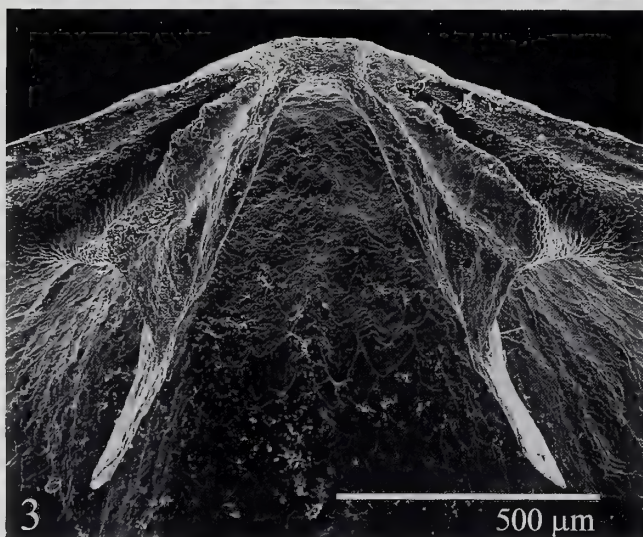
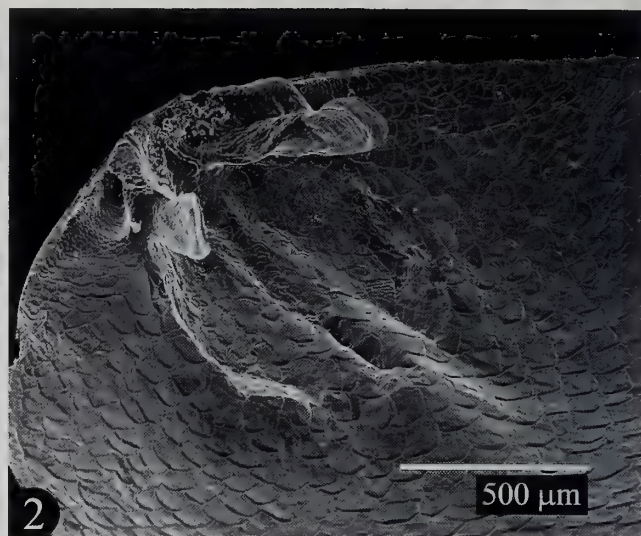
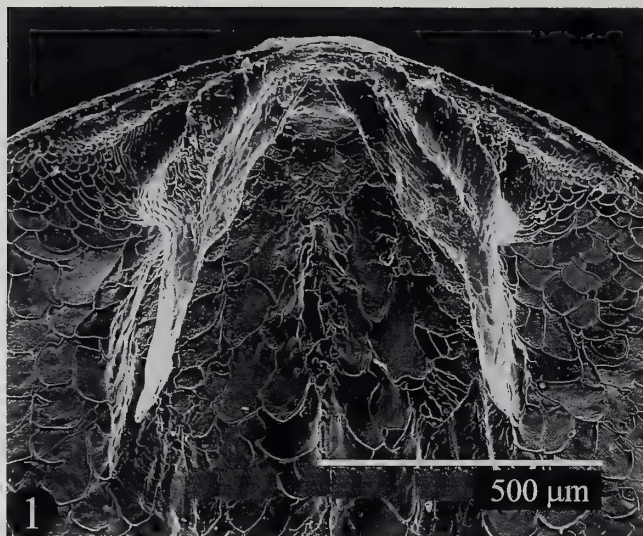
a member of a cryptic brachiopod-sclerosponge community, but never found from the innermost part of the closed cave that does not have sufficient water movement. So far, fresh empty shells of *P. cavernicola* are limited to the sediments from within the caves and only a single fragmentary shell was collected from sediments outside the caves. Thus, *P. cavernicola* should be regarded as typically a cave-dweller. Brachiopods associated with *P. cavernicola* include: *Craniscus* cf. *japonicus*, *Terebratulina* sp., *Argyrotheca* sp.1, *Argyrotheca* sp.2, *Frenulina sanguinolenta*, 'Frenulina' sp., 'Amphithyris' sp., *Thecidellina* sp. and *Lacazella* sp. (Saito *et al.*, 2000). Dead shells of *P. cavernicola* were most abundant in 'Nakanoshima Hole' cave, where the holotype was collected. In this cave *P. cavernicola* represents 11.2% of the total (N = 116) of the brachiopod dead shell assemblage. Corresponding figures for other brachiopods in the same cave are: *Craniscus* -11.2%, *Argyrotheca* sp.1 -14.7%, *Argyrotheca* sp.2 -0.9%, *Frenulina sanguinolenta* -1.7%, 'Frenulina' sp. -47.4%, *Thecidellina* sp. -1.7% and *Lacazella* sp. -11.2%. All those cave brachiopods are characterized by a minute adult shell size, usually less than 5 mm in length, which could have resulted from employment of the same adaptive strategy to the dark and oligotrophic environment as advocated for other cave-dwelling brachiopods, including the rhynchonellide *Tethyrhynchia* from the Mediterranean caves (Logan and Zibrowius, 1994; Simon and Willems, 1999), and cave molluscs (Kase and Hayami, 1992; Hayami and Kase, 1996).

**Diagnosis.**—*Parasphenarina* with abraded rounded ventral beak and poorly defined dental plates; teeth and dental sockets not corrugated. During ontogeny inner hinge plates appear in juveniles but are almost completely resorbed in adult individuals. Outer hinge plates appear in mid-sized specimens and develop gradually during ontogeny to reach their maximum size in adult and gerontic specimens.

**Description.**—Shell diminutive, impunctate, translucent, delicate, teardrop-shaped to rarely oval in outline, longer than wide, equibiconvex or dorsibiconvex. Maximum observed length (L) -6.20 mm, width (W) -5.51 mm, and thickness (T) -3.54 mm. Maximum width and thickness at midvalve; anterior commissure rectimarginate; lateral commissures straight. Surface smooth, with well defined growth lines; in adult specimens better developed anteriorly

← **Figure 4.** *Parasphenarina cavernicola* gen. et sp. nov. Shimoji Islet, Miyako Island. 1. Interior of a ventral valve to show the sessile pedicle collar and heart-shaped muscle field, specimen UMUT RB28220-R5-11, 'Nakanoshima Hole'. 2. Interior of a ventral valve showing the sessile pedicle collar, teeth and dental plates, specimen UMUT RB28219-R2-3, 'Coral Hole'. 3. Detail of 2 showing the left tooth, dental plate and the narrow umbonal cavity. 4. Detail of 2 showing the right tooth, dental plate and the narrow umbonal cavity. 5. Umbonal part of a large ventral valve showing close disjunct deltidial plates, UMUT RB28220-R2-9. 6. The same valve from 5, inclined to show the large teeth and pedicle collar lying on the valve floor.







with slight imbrication laterally. In many specimens umbonal part of shell, just anterior to smooth protingular node, finely capillate (Figure 3.1–3.3). Beak almost straight, foramen hypothyrid, large, deltidial plates disjunct, auriculate (Figure 3.1, 3.4, 3.6). Ventral beak abraded, due to migration of pedicle towards ventral valve; foramen thus has a rounded tip (Figure 3.1, 3.3, 3.4, 3.6). Beak ridges not defined.

Ventral valve interior with short but elongate, uncorrugated, large teeth (Figure 3.4), supported by incipient, short, divergent dental plates, developed close to shell wall, forming shallow, narrow umbonal cavities (Figure 4.1, 4.3, 4.4). Pedicle collar large, elevated above valve floor forming a chamber beneath, with well defined growth lines (Figure 4.1–4.4). Muscle field large, heart-shaped (Figure 4.1, 4.2), occupying 1/4 to 1/3 of shell length. No pallial markings.

Dorsal valve interior with uncorrugated dental sockets, bounded by well developed socket ridges. Inner socket ridges thick; no cardinal process. Crura of spinuliform type, short blade-like (Figure 5.3–5.6), often widening like a spade at their distal ends (Figure 6.2, 6.4). Juvenile specimens have inner hinge plates (Figures 5.1, 11.1); adult specimens develop outer hinge plates, inclined dorsally to shell floor (Figure 5.3, 5.5). Relatively large circular muscle field defined by distinct slopes laterally. In this field there is a shallow median groove bounded by two low ridges from sides (Figure 5.2). No pallial markings visible. Compared to muscle field of other frieleiid genera musculature of this genus is feeble, correlating closely with reduced size.

Serial sections of an adult specimen embedded in epoxy show clearly divergent plates, narrow umbonal cavities, close to lateral wall and strong teeth (Figure 7). In dorsal valve, outer high plates dorsally inclined and spinuliform crura arise from dorsal side of hinge plates. Anteriorly, crura with weak crescent shape sections (convex outward). Median groove very weak and sinuated in centre between two low ridges in muscle field, outlined by lateral slopes.

Majority of living individuals juvenile. Lophophore rarely preserved, of a schizolophous type in a specimen 1.8 mm long with long setae present (Figure 8.1). Largest living specimen ( $L = 5.45$  mm) with a spirolophous-type lophophore, but its shape, number of volutions and orientation unknown due to mechanical distortion. Mature gonads observed in posterior part of mantle in same specimen

(Figure 8.2).

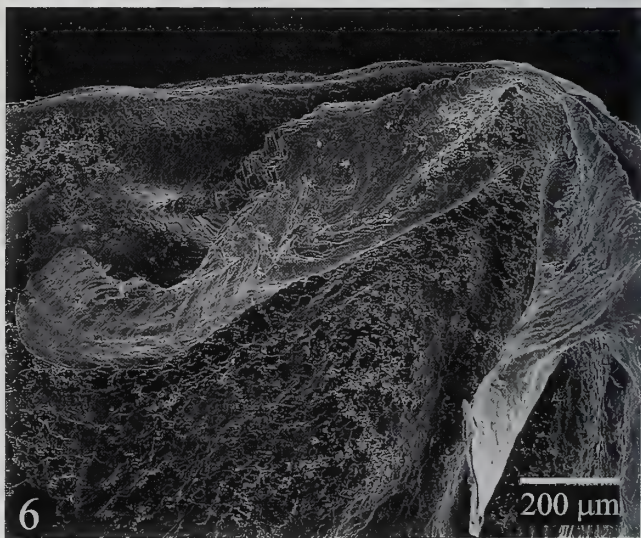
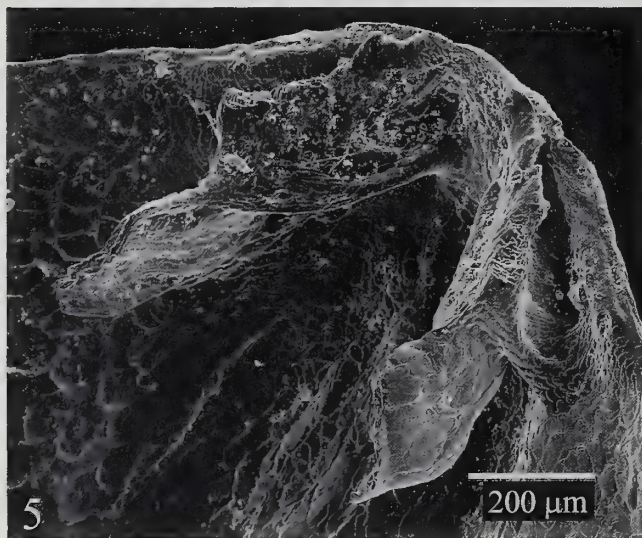
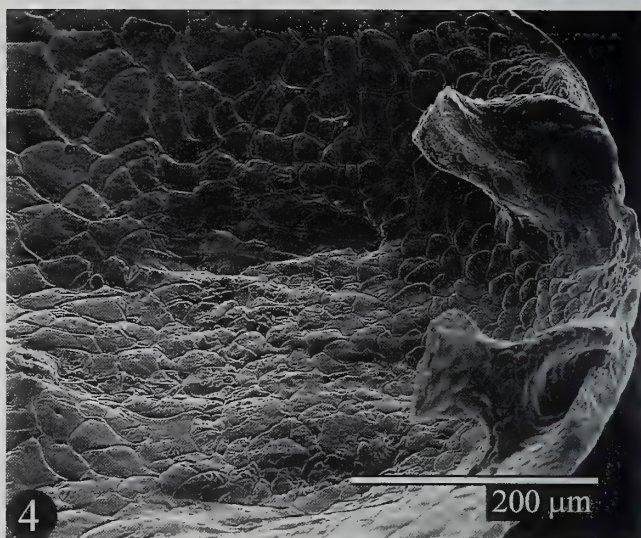
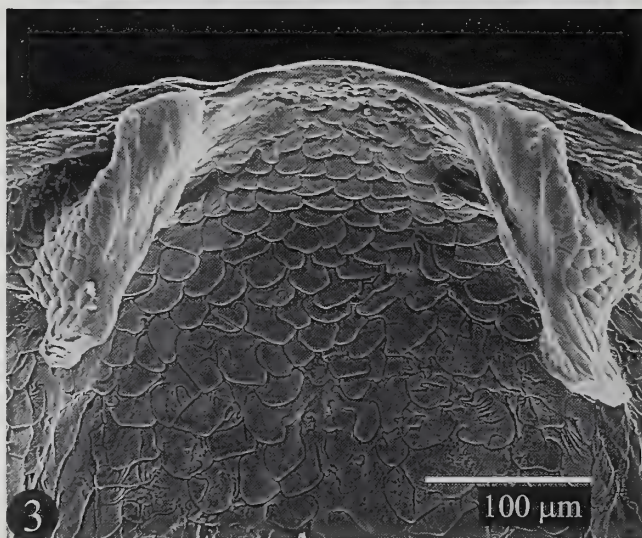
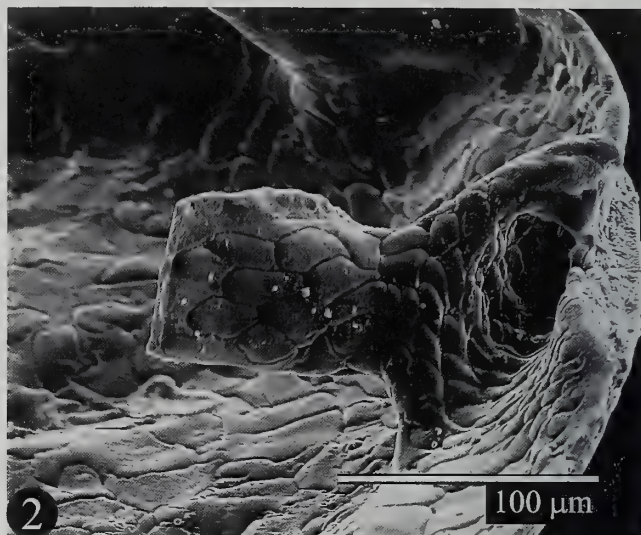
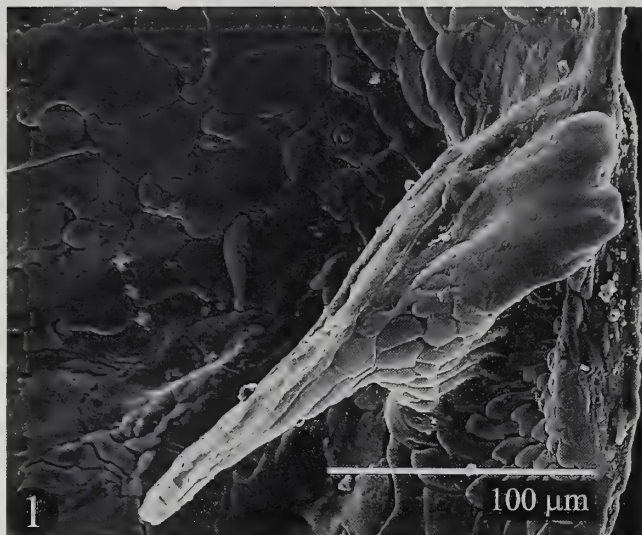
*Measurements.*—Length ( $L$ ), width ( $W$ ) and thickness ( $T$ ) of all the intact specimens (except the living ones) were measured. The living individuals were measured for length and width only. Scatter graphs for  $L/W$  and  $L/T$  show more or less linear relationships (Figure 9A). Slopes of the regression lines for double-logarithmic scatter plots (Figure 9B) based on reduced major axis (Kermack and Haldane, 1950) were 0.99 and 1.12 for  $L/W$  ( $N = 126$ ) and  $L/T$  ( $N = 70$ ), respectively, and both were not significantly different from the slope of 1 (isometry) at the 95% confidence level.

*Intraspecific variability.*—The majority of the adult specimens have a teardrop outline (Figure 2), but some specimens are oval. The growth lines are well expressed in the majority of individuals, but some have weaker growth lines. Some individuals have well defined capillae just anterior to the smooth protingular node. This is better expressed in the dorsal valves (Figure 3.1–3.3). Some shells do not have well defined muscle fields in both valves, while others do. The cross sections of the crura are quite variable. Usually they represent straight thin vertical lamina or have slight crescent-shaped sections convex outward (Figures 5.1, 6.2, 7). In some specimens the crura are curved longitudinally, similar to falciform (Figure 6.5) or are gently sigmoidal anteriorly (Figure 5.6).

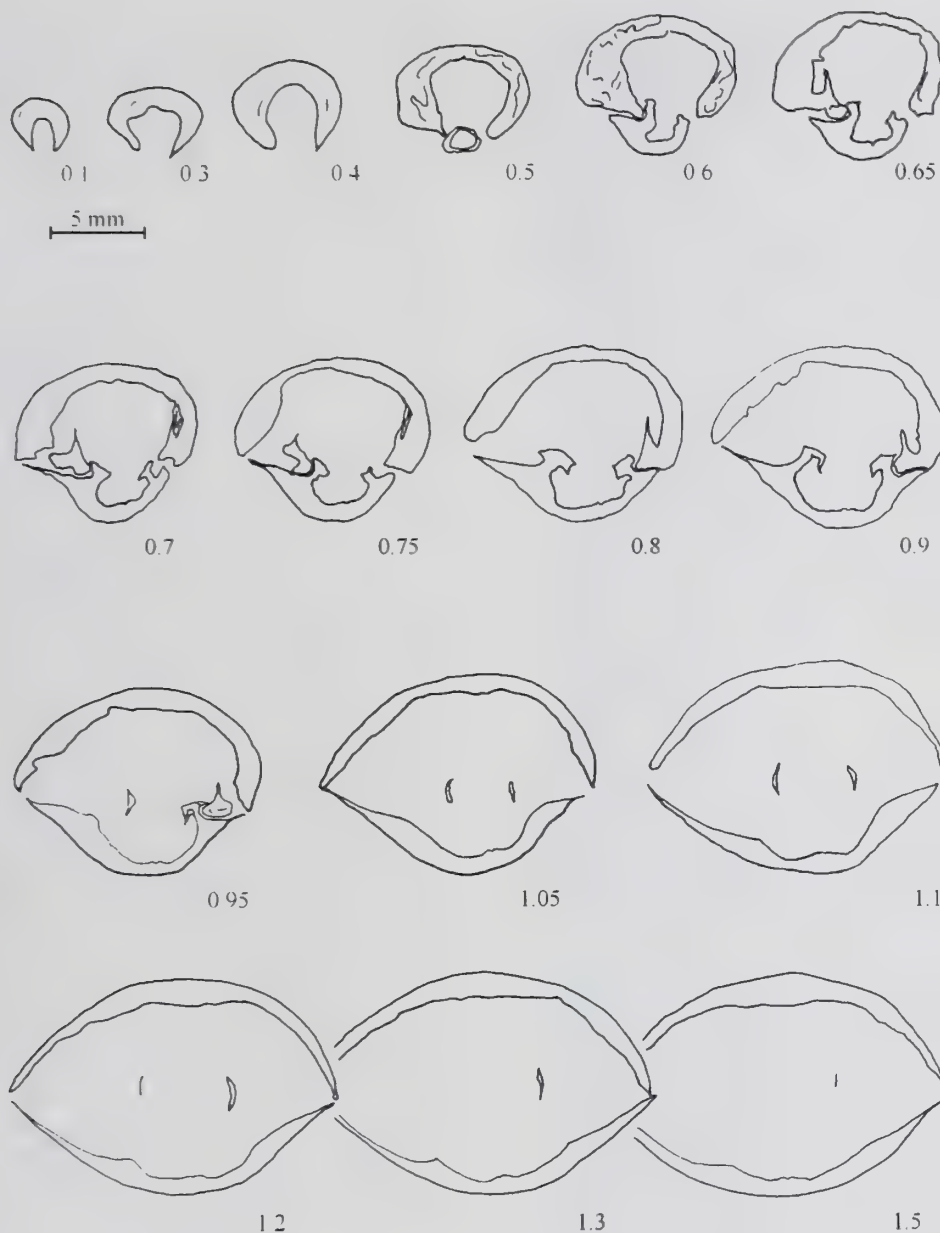
*Ontogeny.*—The smallest individual collected is 0.88 mm long and 0.73 mm wide. The variability of the cardinalia was studied in a sequence of 17 dorsal valves of different size, representing different ontogenetic stages (Table 1). The smallest dorsal valve is 0.92 mm long and 0.92 mm wide, and the largest one examined is 5.51 mm long and 5.37 mm wide. It was noticed that the smallest specimens (early juveniles) have slight or no inner hinge plates and no outer hinge plates (Figure 6.1, 6.3). The juvenile specimens between 1.4 and 2.7 mm length have well defined inner hinge plates but no outer hinge plates (Figures 5.1, 11.1), the crural bases being directly attached to the inner socket ridges. In juvenile and mid-sized specimens the inner socket ridges are swollen posteriorly. With increasing age the socket ridges decrease relatively in size and remain well defined, but not swollen. Dorsal valves, more than 3 mm in length, already have incipient outer hinge plates, inclined to the shell floor. The larger the valve is, the longer and better expressed the outer hinge plates are, and they become inclined to the shell floor

← **Figure 5.** *Parasphenarina cavernicola* gen. et sp. nov. Shimoji Islet, Miyako Island, 'Nakanoshima hole'. Cardinalia of three different-sized dorsal valves. For dimensions of the valves see Table 1. 1. Interior of middle-sized dorsal valve showing crura and well developed inner hinge plates, UMUT RB28220-R1-12. 2. The same valve from 1 showing the median groove between two ridges. 3. Cardinalia of a larger specimen showing well developed outer hinge plates, UMUT RB28220-R1-3. 4. The same specimen as on 3 showing lateral view of the crura. 5. Cardinalia of large specimen showing well developed outer hinge plates, UMUT RB28220-R1-8. 6. The same specimen from 5 showing the crura anterolaterally.



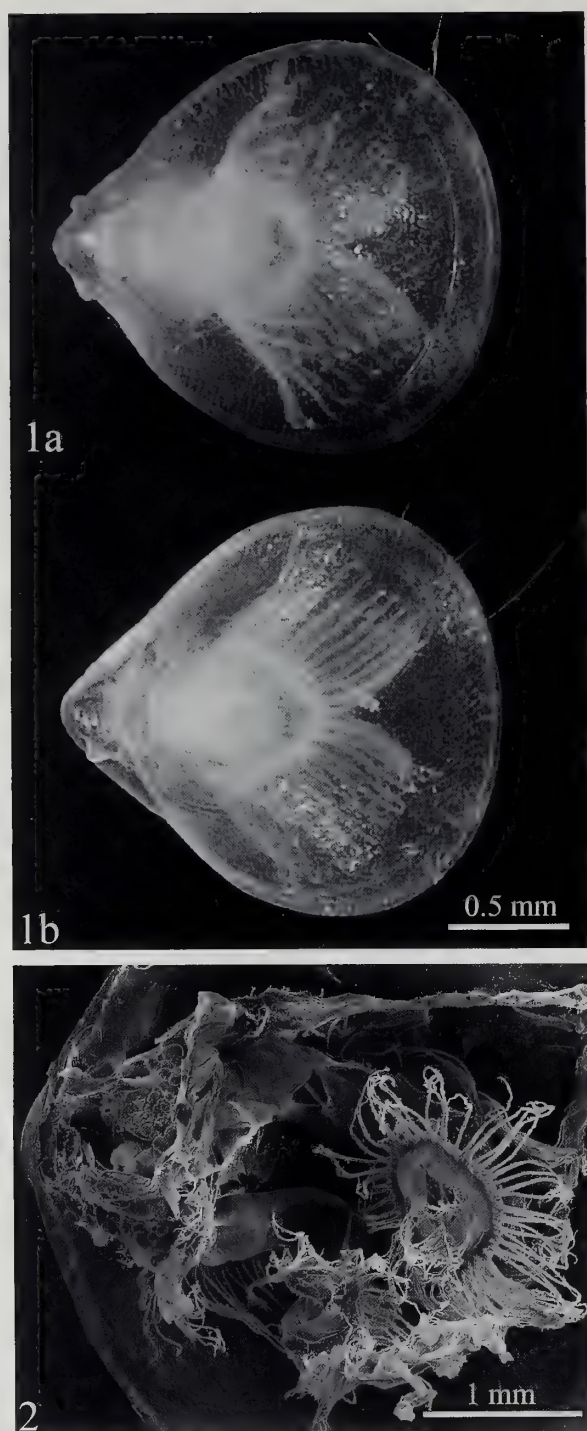






**Figure 7.** Sixteen quasitransverse serial sections through the umbo of *Parasphenarina cavernicola* gen. et sp. nov. Specimen UMUT RB28220-MN01-c. 'Nakanoshima hole' Shimoji Islet, Miyako Island. L = 4.5 mm, W = 4.1 mm; T = 2.3 mm. Distance from ventral umbo given in mm. The asymmetry of the sections is due to the slight lateral inclination of the minute shell during sectioning.

← **Figure 6.** *Parasphenarina cavernicola* gen. et sp. nov. For dimensions of the dorsal valves see Table 1. **1-5** Specimens from Shimoji Islet, Miyako Island, 'Nakanoshima hole'. **1.** Juvenile crus, swollen inner socket ridge and incipient inner hinge plate seen in the commissural plane, UMUT RB28220-R5-4. **2.** The same crus as on **1**, seen laterally to show the spadeline shape. **3.** Cardinalia of juvenile specimen, UMUT RB28220-R5-9. **4.** The same valve from **3** seen laterally. **5.** Cardinalia of a middle-sized specimen with crescent-shaped crura and inner hinge plates, UMUT RB28220-R1-10. **6.** Cardinalia of adult or gerontic specimen showing the ventral curving of the distal ends of the crura, specimen from a mixed sample UMUT RB28213-R9 from 'Shodokutsu' and 'Daidokutsu' caves, Ie Islet, Okinawa Islands.



**Figure 8.** *Parasphenarina cavernicola* gen. et sp. nov. 1. Setae and schizolophous lophophore in juvenile specimen seen through the transparent shell. 1a, ventral side. 1b, dorsal side. Specimen UMUT RB28214-MD03-a, "Devil's Palace", Shimoji Islet, Miyako Island. 2. Distorted spirolophous lophophore in larger specimen. Mature gonads are seen in the posterior part of the mantle. Specimen UMUT RB28212-ID11-a, 'Daidokutsu' cave, Ie Islet, Okinawa Islands.

(Figures 5.3, 5.5, 7).

The crura in the juvenile specimens are shorter and slightly curved ventrally with spadelike anterior tips (Figure 6.2, 6.4). As pointed out by Dagys (1974), during ontogeny spinulifer crura simply increase in size. However, some larger specimens show characteristic stronger ventral bending of the distal ends of the crura (Figures 5.6, 6.6). The median dorsal groove between two low ridges is present in all stages except the early juvenile and with age it becomes better defined.

The juvenile ventral valves do not have dental plates detached from the shell wall, so the umbonal cavities are still not developed. The teeth are relatively large in juvenile specimens. During growth dental plates appear and start detaching from the lateral wall of the umbo. In adults they are well defined, but remain close to the wall, delimiting narrow umbonal chambers (Figure 4.1–4.4). With age the teeth become elongate in the commissural plane, but remain low perpendicular to this direction (Figure 4.5, 4.6). The juvenile individuals have well developed winglike deltidial plates (Figure 3.1, 3.6). In adults the deltidial plates are sometimes resorbed, but some specimens show excessive growth. In the largest ventral valve ( $L = 5.7$  mm), the deltidial plates are very close to each other and the pedicle collar lies on the valve floor (Figure 4.5, 4.6).

**Shell ultrastructure.**—The shell ultrastructure of *Parasphenarina cavernicola* was observed using SEM by different preparation methods. The shell is very thin: maximum 300  $\mu\text{m}$  in the centroanterior part. Laterally it is thinner and reaches 20  $\mu\text{m}$ . It consists of two calcite layers, primary and secondary.

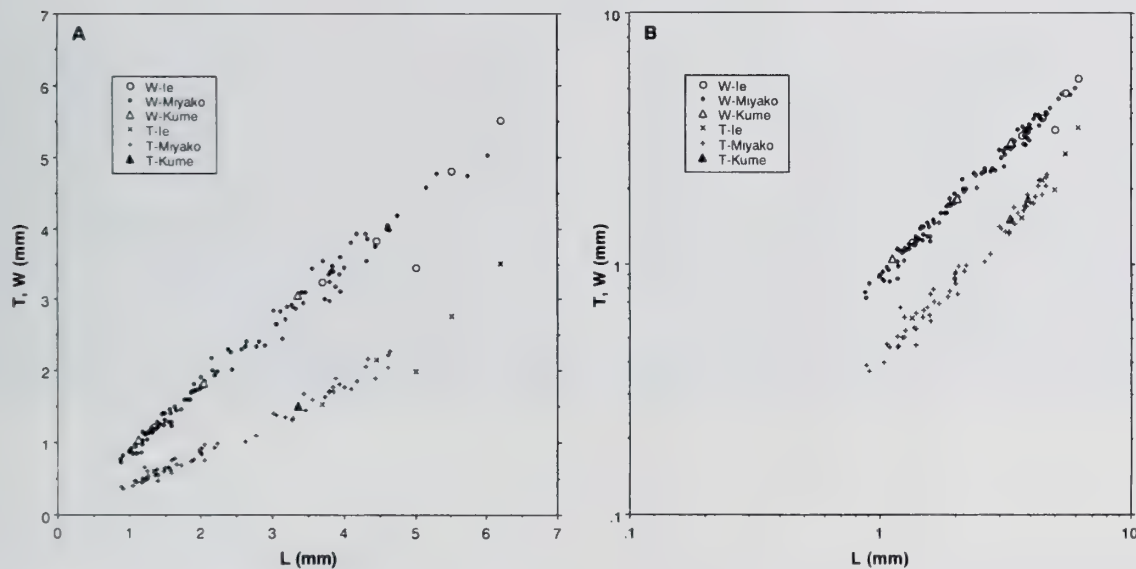
In some cases the periostracum was preserved on the shell surface, but for examining the microstructure of the external surface of the primary layer it was removed using domestic grade bleach as described in the previous section. Thus, its negative impressions on the external surface of the primary layer were revealed (Figure 10). They represent subparallel labyrinthine trenches normal to the growth lines of the shell. Such casts have been observed in different orders of brachiopods and were recently reappraised by Williams (1997, in Kaesler, 1997, p. 269–271).

The primary layer is 5 to 10  $\mu\text{m}$  thick. It is built up of parallel rodlike calcite aggregates normal to the shell surface, which according to the method of treatment of the sample and the angle of observation can have different aspects, some of them illusory. The most typical texture of the primary layer observed is the vertical (normal to the bounding surfaces of the primary layer) (Figures 11.3, 11.4, 11.6, 12.2–12.4). It reflects the orientation of the parallel rodlike aggregates of calcite crystallites. The tips of the individual rodlike crystallites are better seen after etching the external surface of the layer (Figure 10.3, 10.4). The growth of the crystallites starts from the boundary between



**Table 1.** Ontogenetic variability of the cardinalia in *Parasphenarina cavernicola* gen. et sp. nov. Ld, length of the dorsal valve; Wd, width of the dorsal valve; Lcr, length of the crura = distance from the posteriormost point of attachment of the hinge plate to the anteriormost part of the crura tip, measured in the commissural plane; all in mm).

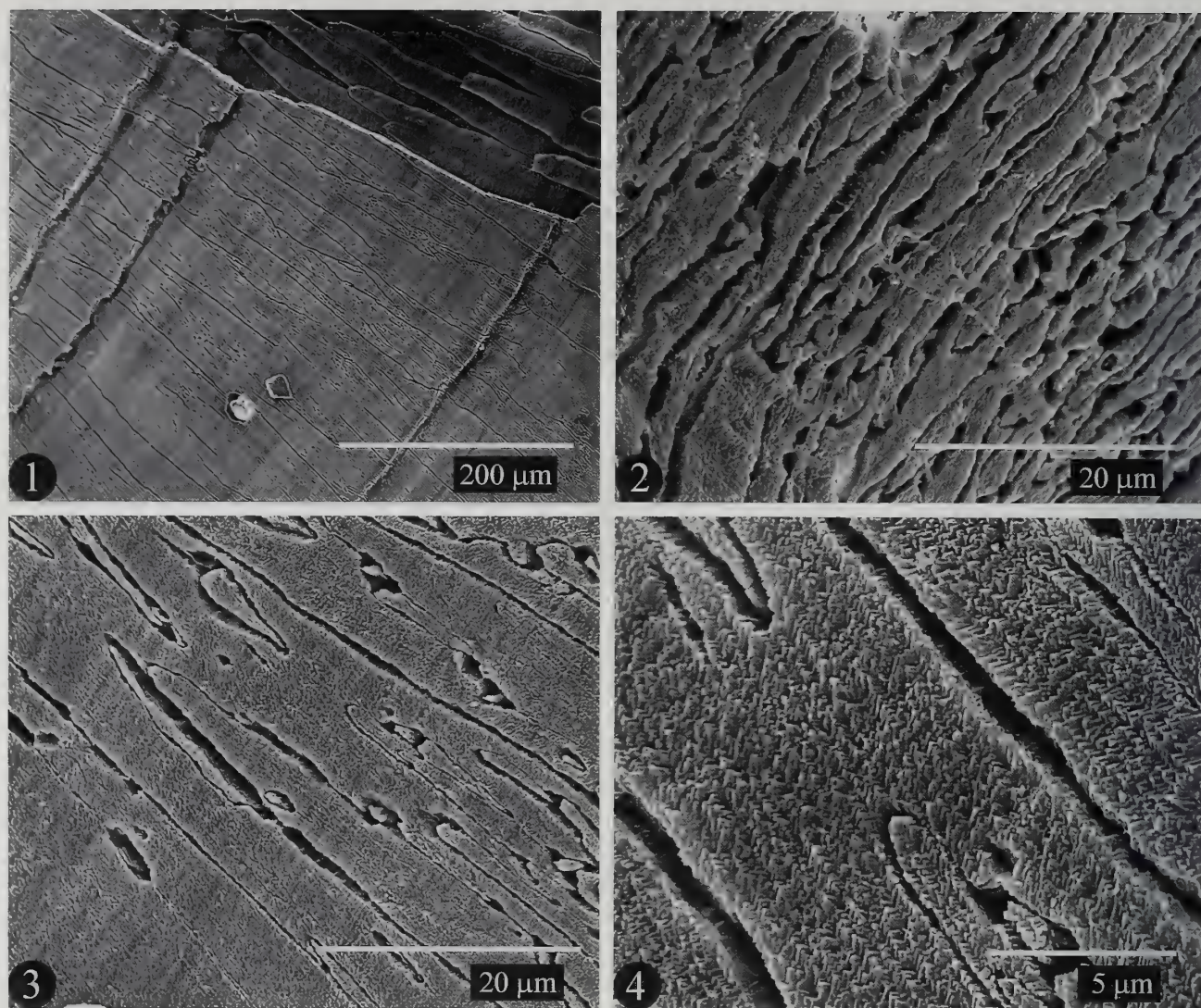
UMUT Specimen No.	Figure	Ld	Wd	Lcr	Inner hinge plates	Outer hinge plates
RB28220-R5-9	6.3, 6.4	0.92	0.92	0.18	?	no
RB28220-R5-1		0.97	0.95	0.26	slight	no
RB28215-R5-2		?	?	0.23	slight	no
RB28220-R5-4	6.1, 6.2	1.02	1.01	0.23	slight	no
RB28220-R5-6		1.03	1.05	0.22	slight	no
RB28215-R3-6		1.4	1.4	0.36	strong	no
RB28219-R2-2	11.1, 11.2	1.47	1.82	0.41	strong	no
RB28220-R5-10		1.9	1.85	0.47	strong	no
RB28219-R4-4		2.71	2.76	0.62	strong	no
RB28220-R1-12	5.1, 5.2	2.71	2.67	0.67	strong	no
RB28220-R1-10	6.5	2.89	2.88	0.61	strong	no
RB28215-R3-5	5.3, 5.4	?	?	0.73	slight	yes
RB28215-R3-2		3.67	3.92	0.79	slight	yes
RB28220-R1-3		3.74	4.34	0.84	??	well developed
RB28219-R2-1	5.5, 5.6	?	?	0.97	slight	short
RB28220-R1-8		4.59	4.69	1.22	?	well developed
RB28213-R9	6.6	5.51?	5.37	1.02	slight	well developed



**Figure 9.** Shell measurements of *Parasphenarina cavernicola* gen. et sp. nov. Scatter plots (A) and double logarithmic scatter plots (B) of shell length (L) versus maximum shell width (W) and thickness (T). Specimens from Ie, Miyako (Irabu and Shimoji islands), and Kume Islands are indicated separately.

the periostracum and primary layer, where the crystallites are finer and not well defined, and advances towards the boundary between the primary and secondary layer. Some micrographs taken at different angles and higher magnification reveal a horizontal texture, which shows a fine lamination parallel to the shell surface and the boundary primary/secondary layer (Figures 11.4, 12.1, 12.2, 12.6). These are surfaces of synchronous growth of the crystal ag-

gregates (induction faces of common growth), which give a laminated aspect to the layer at high magnification. *Parasphenarina cavernicola* differs from *Notosaria nigricans* (Sowerby) in the parallel orientation of the synchronous growth surfaces. *Notosaria nigricans* develops its synchronous surfaces oblique to the two boundaries (Williams, 1971). An unusual pseudo-porcelain appearance, probably an artifact due to over coating with Pt-Pd



**Figure 10.** Views of the external surface of the primary layer of *Parasphenarina cavernicola* gen. et sp. nov., 'Nakanoshima Hole', Shimoji Islet, Miyako Island. **1, 3, and 4** specimen UMUT RB28220-ss3-vv, fragment of a dorsal valve, treated with 5% v/w bleach for 13h and etched with 5% HCl for 5sec. **1.** General view of the external surface of the shell (respectively of the primary layer). Three growth lines are visible. In the top right corner the primary layer is broken off and the underlying fibres are visible. The trenches perpendicular to the growth lines represent negative casts of periostraca dissolved by bleach. **2.** Specimen UMUT RB28220-ss4-vv, fragment of a ventral valve, treated with 5% v/w bleach for about 3h and over etched with 5% HCl for longer period-15sec. Labyrinthine trenches are overetched impressions of periostraca casts in the primary layer. **3.** Detail of **1.** **4.** Detail of **3.** Tips of spiky calcite crystallites.

alloy, was observed on some spots of the primary layer (Figure 12.5).

The large fibres of the secondary shell, arranged in orthodox fashion, form a mosaic on the internal part of the valves (Figure 11.2). The fibres are usually rhombic in cross section. They are extraordinarily large: 50–100 µm in width and 20–40 µm in thickness. Near their origin (the boundary with the primary layer) the fibres are smaller (40–60 µm wide and 15–25 µm thick) and represent well

shaped rhombi. They expand rapidly towards the interior of the shell (80–140 µm wide and 30–40 µm thick), losing their regular rhombic shape and becoming irregular rhombi, polygons, or anvil-shaped and sometimes have rounded margins (Figure 11.3, 11.5, 11.6).

Among other genera with spinuliform crura, scanty data on the shell ultrastructure are illustrated on *Manithyris rosii* Foster, *Compsothyris racovitzae* (Joubin) and *Compsothyris ballenyi* Foster (Foster, 1974, pl. 9). The width of the



fibres on the internal surface of the ventral valve is 50  $\mu\text{m}$  in *Manithyris rosii* and 40  $\mu\text{m}$  in *Compsothyris*. Compared to the fibres of *Parasphenarina cavernicola*, the fibres in *Manithyris* and *Compsothyris* are narrower and the mosaic they form is different. Popov (1978) published 3 micrographs from different parts of the internal surface of the shell of *Frieleia halli* Dall showing fibres differing in size and morphology. Two of the micrographs show peculiar terminal faces of the fibres wrinkled parallel to the long axes (Popov, 1978, figs 1b–d).

A. Williams provided for comparative study five micrographs showing the shell ultrastructure of two fragments of *Frieleia halli*. In addition he commented (personal communication, 2000) on the peculiarities of the ultrastructure of this species: The external surface of the primary layer is sporadically pitted, probably by the imprints of the mucin-filled vesicles within the infrastructure of the periostracum (Figure 13.2). The primary layer seems finely laminated at high magnification (Figure 13.3), as described above for *Parasphenarina cavernicola*. At lower magnification the primary layer is crossed by nearly vertical planes, which are also comparable to the edges of the aggregates of parallel rodlike crystallites described above (Figure 13.2). The shell mosaic is somewhat different (Figure 13.1). The fibres are 40–50  $\mu\text{m}$  wide, extremely flat and unusual in the way the apices of the terminal faces appear to be wrinkled parallel to the long axes of the faces (Figure 13.1), similar to that figured by Popov (1978).

Thus, the shell ultrastructure in the family Frieleidae appears coarsely fibrous although more data are needed to draw conclusions about the taxonomic importance of ultrastructure in frieleiids in particular, and in the Norelloidea as a whole (cf. Manceñido and Owen, 2001 for a new rhynchonellid classification). It is noteworthy that a similar coarse-fibrous fabric has been already reported in Cretaceous Pugnacoidea, in contrast to the fine-fibrous ultrastructure in Cretaceous Rhynchonelloidea and Hemithyridioidea (Mochurova-Dekova, 2001). However, it should be noted that shell ultrastructure might be influenced by water temperature and other environmental factors as well. The coarseness of the mosaic and other ultrastructure features are probably largely genetically determined phenotypic changes favoured by natural selection in a particular environment over a long period of time but may also be evoked somatically (without change of genotype) by the same environmental conditions in the short term (M. Foster, personal communication, 2002). It is necessary to make quantitative studies of a large number of specimens of many different species from a wide variety of habitats to make sound observations and conclusions.

**DNA sequence data.**—Mitochondrial cytochrome c oxidase subunit I (cox1) gene sequence, DDBJ accession

number AB053201 (Saito *et al.*, 2001).

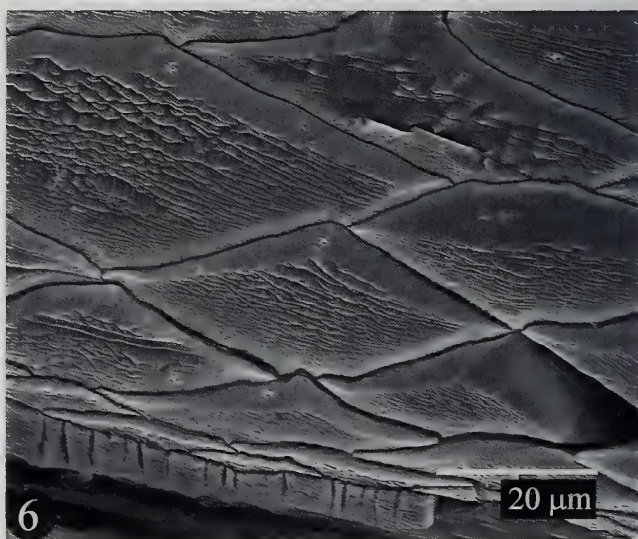
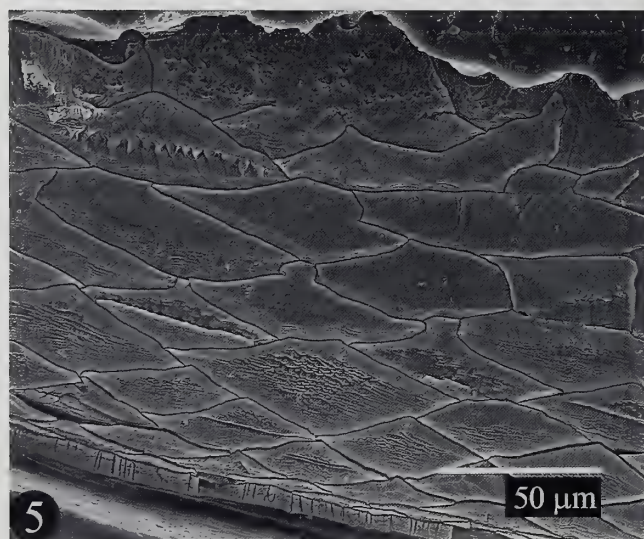
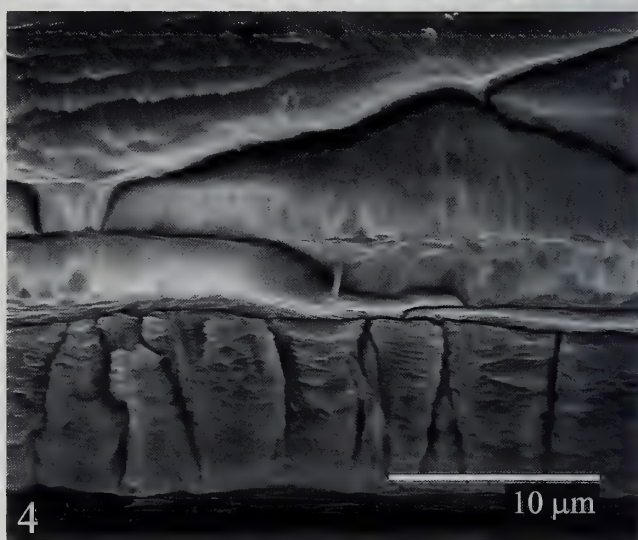
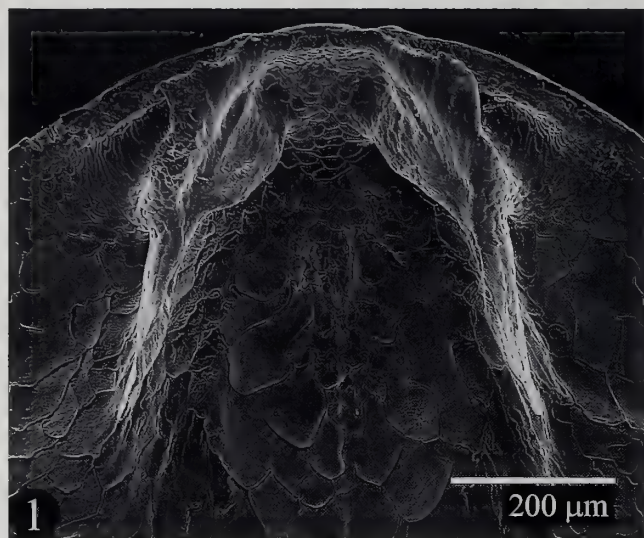
**Comparison.**—*Parasphenarina cavernicola* closely resembles *P. ezogremena* (Zezina) in size, shape of the shell and crura and in having a shallow median groove bounded by low ridges in the dorsal valve instead of a typical median septum. *Parasphenarina ezogremena* differs from *P. cavernicola* in having a well defined larger triangular foramen with pointed acute beak. It lacks the characteristic abraded rounded ventral beak of *Parasphenarina cavernicola*. *P. ezogremena* has corrugated socket ridges and teeth, supported by stronger dental plates, while socket ridges and teeth are smooth and dental plates are poorly developed in *Parasphenarina cavernicola*. After examining several specimens of the new rhynchonellid from the Okinawa submarine caves, Zezina (personal communication, 2000) also suggested they be placed in a new species to distinguish them from *Parasphenarina ezogremena* (Zezina).

*Parasphenarina cavernicola* sp. nov. resembles *Sphenarina sicula* Davidson in the shape of the shell and crura (Figure 14.1) and the rectimarginate anterior commissures. The umbonal part of *P. cavernicola*, just anterior to the smooth protegular node, is finely capillate, which is reminiscent of the fine capillation of the entire shell of *S. sicula*. The main differences are given in the comparison between the two genera. *Parasphenarina cavernicola* differs from *Sphenarina sicula* in being smaller in size, completely smooth, with well developed growth lines, a larger foramen, consistently disjunct deltidial plates, relatively larger teeth, and very narrow umbonal chambers in the ventral valve, limited by slightly developed divergent dental plates. These are differences that could be also of specific importance. The most important difference between the two species (and genera) is in the cardinalia. The cardinalia of *Sphenarina sicula* are relatively more massive, have an incipient cardinal process, the hinge plates and inner socket ridges join together posteriorly (Figure 14.1), and a small septalium is present in the sectioned adult shell (Figure 14.2). In *Parasphenarina cavernicola* the hinge plates and socket ridges remain separate (Figures 5.1, 5.3, 5.5, 6.3) and touch the valve floor, which together with the lack of a median septum totally excludes the possible formation of a septalium. In *S. sicula* the crural bases project more ventrally than dorsally in adult shells (Figure 14.3), while in *Parasphenarina cavernicola* the crural bases project dorsally only (Figures 5.3–5.6, 7).

## Discussion

The abundance of material, representing populations of *Parasphenarina cavernicola* inhabiting different caves, allows us to study in detail the intraspecific variability and the ontogeny of the shells. Such studies aid in preventing







undue the taxonomical splitting that often arises when new species and genera are erected only on the basis of scarce material. As pointed out by Foster (1974), genera have customarily been too narrowly defined in the rhynchonellides. Some of the genera were monospecific when they were erected. Thus, their diagnoses coincided with the diagnoses of the type species. Including new species in such monospecific genera is always difficult. In the case of *Parasphenarina cavernicola* we have preferred to introduce a new genus rather than to emend the diagnosis of the closest genus *Sphenarina*, based on the absence of a septalium in the new genus. Another hampering factor was the lack of previous ontogenetic observations on the known species belonging to the Frieleidae, except for Foster (1974), where he commented on the ontogeny of *Compsothyris racovitzae* (Joubin). As a whole, the rhynchonellides are considered as a group with primitive cardinalia and their possible ontogenetic changes were normally neglected.

Several authors in the past have drawn attention to the need to include in taxonomic descriptions detailed accounts of growth stages (Surlyk, 1972; Lee and Wilson, 1979). A detailed account of the growth stages in *Notosaria nigricans* was given by Lee and Wilson (1979). Manceñido and Walley (1979) point out the inadequacy of a classification based on the mere presence or absence of a morphological feature in the adult stage. They recommend erection of new taxa on the basis of both juvenile and adult morphology and inclusion of this in the diagnosis.

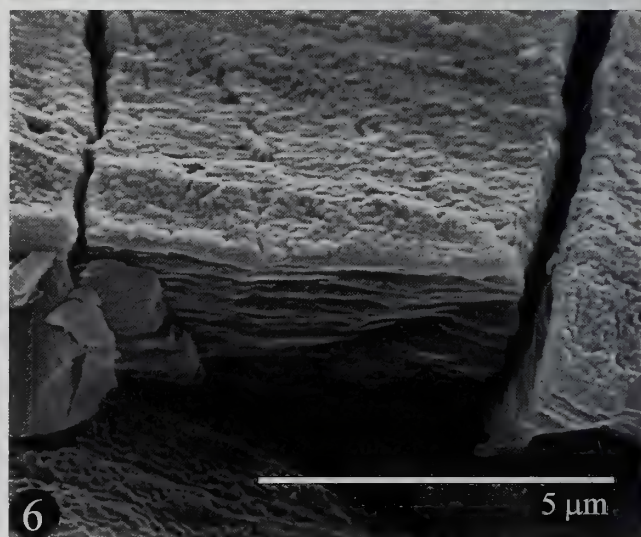
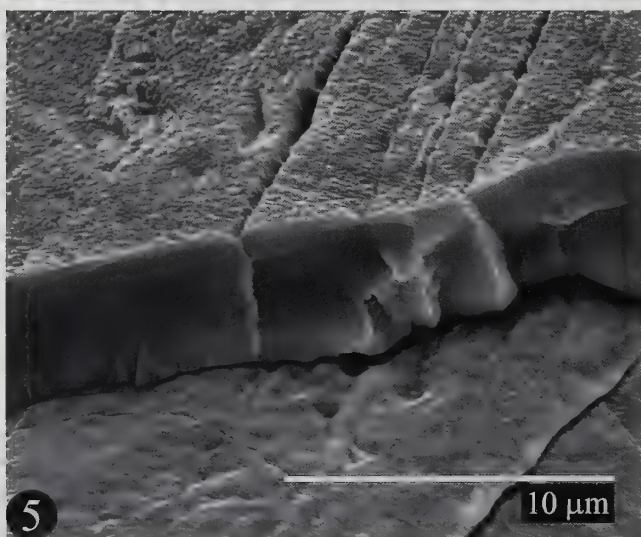
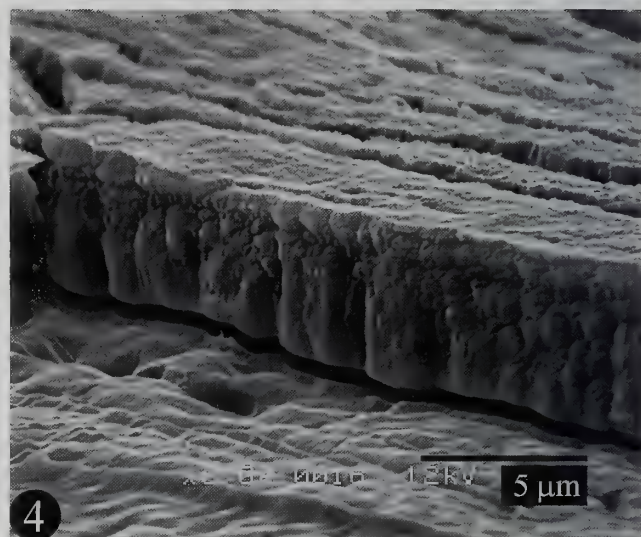
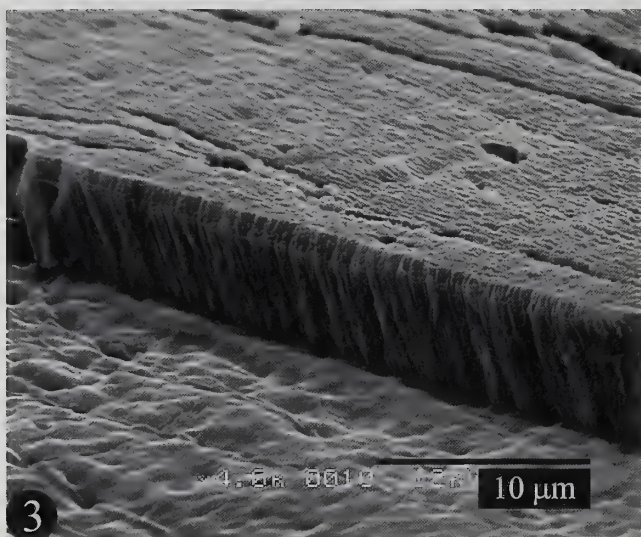
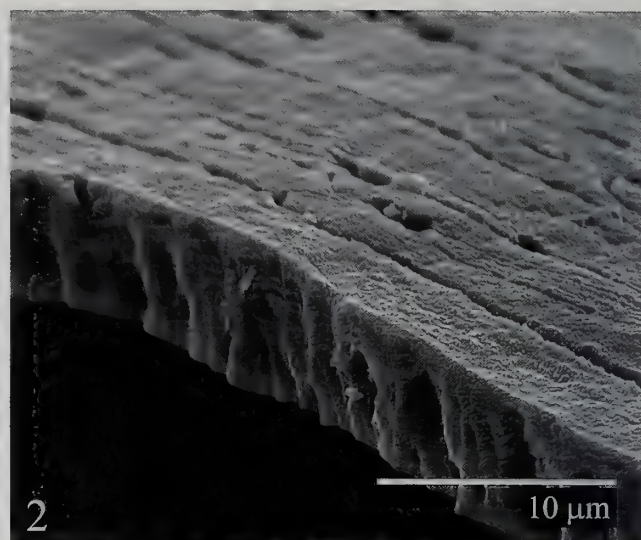
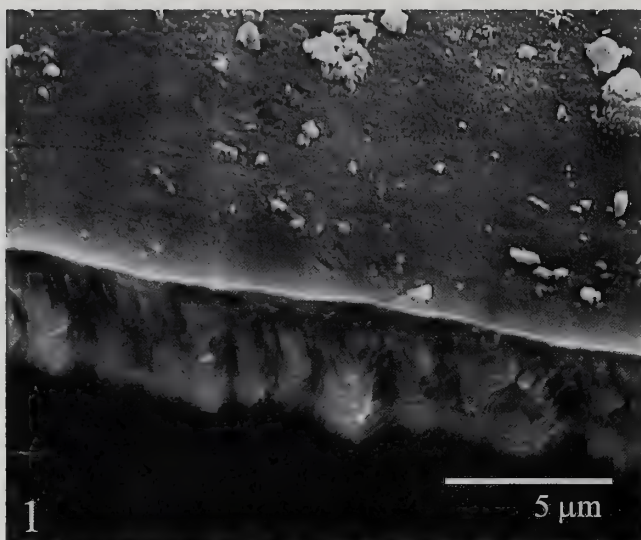
One important discovery resulting from this study was that the morphology of the hinge plates changes considerably during ontogeny. The morphology and the lack or presence of inner and outer hinge plates are often taken as a diagnostic generic character. After a careful examination of dorsal valves of different size of *Parasphenarina cavernicola*, it turned out that the inner hinge plates are present only in juvenile shells, later being resorbed or transformed. The outer hinge plates develop later and are well defined only in the adult shells. Thus, examining scarce material, not representing all the stages, may lead to misidentification or overestimation of some of the cardinalia features in rhynchonellides. In this instance we consider that too many genera were introduced on the basis of insufficient material. In this case we suggest that genera established on presence/absence of inner/outer hinge plates or

absence of septalium (for instance *Sphenarina*) should be carefully revised.

According to Dagys (1974) spinuliform crura appeared in different groups of rhynchonellides as a result of 'fetalization' (i.e. paedomorphosis). Genera having spinuliform crura retain some juvenile aspects in the adult stage. Dagys (1974) noted that such genera are characterised by a triangular outline, weak to moderate convexity, lack of a sinus, and unisulcate to rectimarginate anterior commissures, which are indicative of juvenile characters in rhynchonellides. Cooper (1959) also noted that the rectimarginate anterior commissure is a youthful character. The adult individuals of *Parasphenarina cavernicola* are micromorphic and bear all of the above-mentioned juvenile characters. On the other hand, *Parasphenarina* has one of the simplest arrangements of cardinalia among rhynchonellides, lacking a septalium and median septum. Thus the occurrence of *Parasphenarina cavernicola* supports Dagys' hypothesis about the paedomorphic nature of the spinuliform crura. *Parasphenarina* can reach sexual maturity at a length of 5.45 mm (Figure 8.2). All these data support the hypothesis that *Parasphenarina cavernicola* can be regarded as a paedomorphically developed form in the submarine caves of Okinawa. The rarity of the new genus in Recent seas is also noteworthy, the only other species, *Parasphenarina ezogremena*, being recorded from a single specimen in the Flores Sea on the upper continental slope (Zezina, 1981). Taking into account the morphologic similarities with the genus *Sphenarina* from Sicily it can be suggested that the new genus could have evolved from forms morphologically close to the extremely rare bathyal Pliocene genus *Sphenarina* through paedomorphosis. Heterochronic processes have probably played an important role in the origination of major new taxa and evolutionary novelties in post-Palaeozoic rhynchonellides. Frieleids were interpreted as end-members of lineages, which become adaptively anachronistic in high-energy environments and eventually occupied refugia in deeper and darker low-energy habitats (Manceñido and Owen, 1996; Manceñido, 1997; Manceñido and Owen, 2001). Considering also the occurrence of associated taxa from other phyla, the new frieleiid *Parasphenarina cavernicola* may be cited as yet another example of an anachronistic taxon with closest bathyal ancestors, which has found refuge in the peculiar low-

← **Figure 11.** *Parasphenarina cavernicola* gen. et sp. nov., 'Nakanoshima Hole', Shimoji Islet, Miyako Islands. 1. Juvenile dorsal valve with well developed inner hinge plates and swollen inner socket ridges, specimen UMUT RB28220 R5-10. 2. Anterior of the dorsal valve of the same specimen as on 1 to show the study surface for the mosaic of the fibres (compare to Figure 13-1). 3-6. Transverse sections at 1.7 mm from the ventral umbo of a ventral valve of the same specimen as on Figure 7. Section thoroughly polished and subsequently etched with 5% HCl for 2-3 sec. 3. Secondary fibrous layer (above) and primary layer (below). 4. Detail of 3 to show the primary layer with the vertical edges of aggregates of calcite and fine horizontal lamination parallel to the shell surface. 5. The whole shell thickness showing the secondary fibrous layer and the primary layer below. 6. Detail of 5 showing the rhombic fibres and the primary layer.





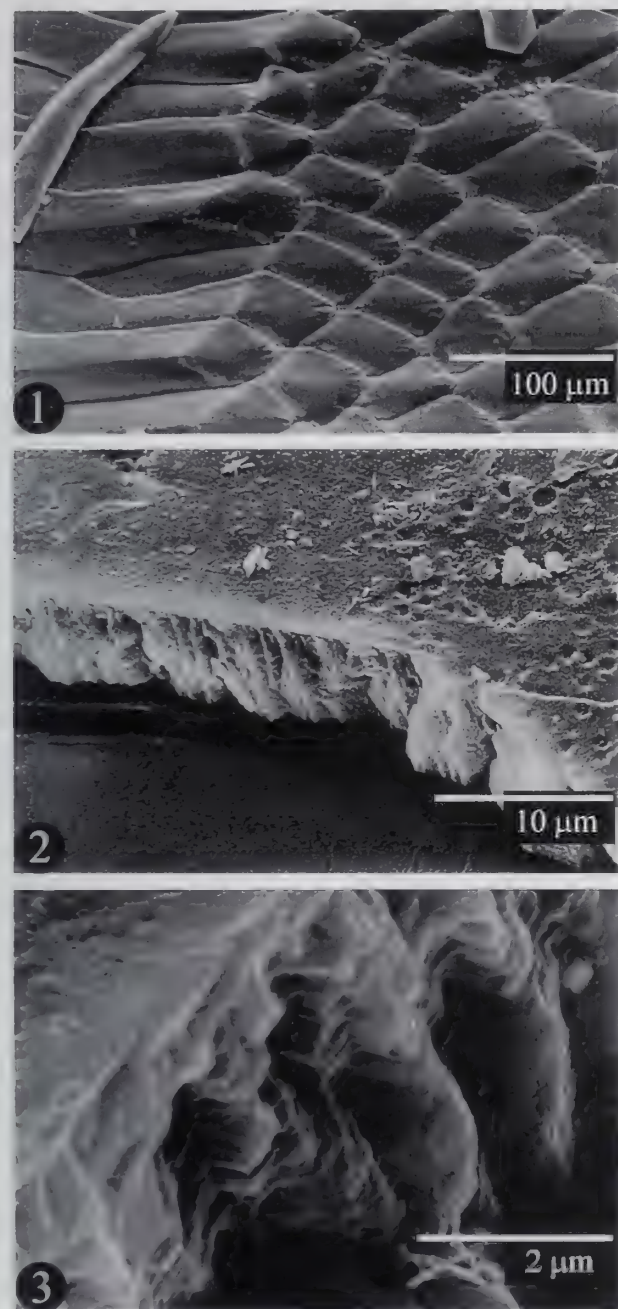


competition, sheltered microenvironment of the dark, oligotrophic submarine caves of Okinawa.

### Acknowledgements

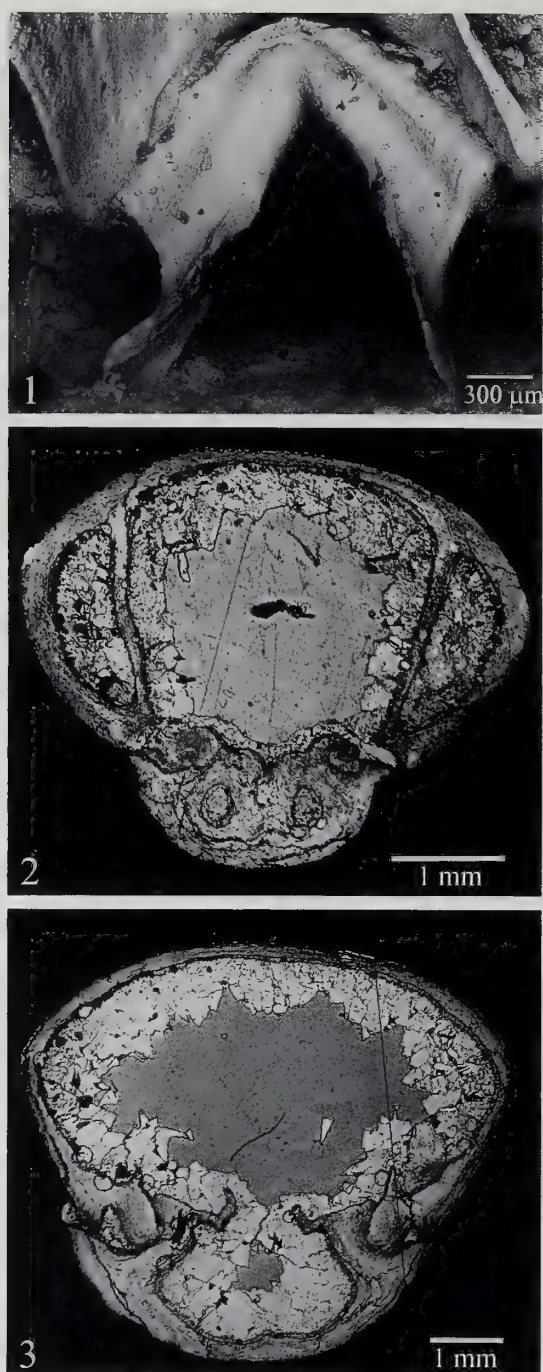
We thank T. Kase (National Science Museum, Tokyo), I. Hayami (Kanagawa Univ.), R. Tabuki (Univ. of Ryukyus) and T. Hanai (Tokyo) for the fruitful fieldwork we conducted together. We are also grateful to the cooperative and skilled divers, S. Ohashi, S. Kinjo (Okinawa) and M. Taniguchi (Miyako Island). O. Zezina (P.P. Shirshov Institute of Oceanology, RAS, Moscow) is thanked for kindly examining specimens of the new rhynchonellide and giving advice. A. Williams (Univ. of Glasgow) kindly commented on shell ultrastructure problems and placed at our disposal micrographs of *Frieleia*. D. Lee (Univ. of Dunedin), E. Owen (Natural History Museum, London), V. Radulović (Univ. of Belgrade), M. Foster (Bradley University, Peoria) gave valuable advice on an earlier version of the paper. We are grateful to the reviewers M. Manceñido (La Plata Natural Sciences Museum) and A. Logan (University of New Brunswick, Saint John) for the insightful and helpful comments. T. Dutro and J. Thompson (Smithsonian Institution, US National Museum) provided us with specimens of *S. sicula* for comparison. M. Gaetani (Univ. of Milan) and D. Saccà (Univ. of Messina) provided valuable information on *S. sicula*. R. Gatto (Univ. of Padua) suggested the new generic name *Parasphenarina*. Zh. Damyanov (Central Laboratory of Mineralogy and Crystallography, Sofia) helped with interpretation of the shell ultrastructure. Special thanks go to K. Moriya, I. Sarashina, T. Sasaki (Tokyo University), M. Ivanov (National Institute of Advanced Industrial Science and Technology, Tsukuba), T. Kodera (Nippon Marine Enterprises, Ltd., Yokohama) and V. Dekov (Univ. of Sofia) for their continuous technical help. N. Motchurova-Dekova gratefully acknowledges the Japan Society for the Promotion of Sciences for her postdoctoral scholarship at Tokyo University. She thanks K. Tanabe for the invitation

**Figure 13.** Ultrastructure of two fragments of *Frieleia halli* Dall shell from the Smithsonian wet collection, USNM 421367, 550 m depth, 32° 40.7' N, 117° 35.5' W, San Diego Trough. **1.** Internal surface of the shell with orthodoxy stacked flat fibres, the apices of the terminal faces of which are wrinkled. **2.** External surface of the shell sporadically pitted. Nearly vertical planes-edges of aggregated of parallel rodlike calcite crystallites. **3.** Finely laminated primary layer, lamination parallel to bounding surfaces at higher magnification.



← **Figure 12.** *Parasphenarina cavernicola* gen. et sp. nov., 'Nakanoshima Hole', Shimoji Islet, Miyako Island. Different textures of the primary layer according to the way of treatment of the sample, the angle of observation and the magnification. **1.** Finely laminated (horizontal) texture. Stub #UMUT RB28220-ss1-dv, treated with 5% v/w bleach for 13h, not etched. **2-6.** Specimen UMUT RB28220-ss3-dv, fragment of a dorsal valve, treated with 5% v/w bleach for 13h and etched with 5% HCl for 5sec. **2.** Horizontal (parallel to the shell surface) lamination and vertical texture. **3.** Vertical texture. **4.** Vertical texture. **5.** Pseudo-porcelain appearance, probably an artifact due to overcoating with Pt-Pd alloy. **6.** Horizontal lamination.





**Figure 14.** *Sphenarina sicula* Cooper. Pliocene, Milazzo (labelled as Milasso), Messina, Sicily. **1.** Cardinalia of specimen USNM 549381a, the same figured by Cooper (1959, p. 8–A, fig.7). Dimensions: L = 12.55 mm, W = 10.50 mm, T = 6.60 mm. Note the incipient cardinal process. **2, 3.** Two acetate peels showing selected serial sections of the interior of a larger specimen #549381b USNM. L = 15.60 mm, W = 15.10 mm, T = 8.40 mm. **2.** Section 2.3 mm from the top of the ventral valve showing well developed divergent dental plates and incipient septalium. **3.** Section 2.9 mm from the top of the ventral valve showing strong teeth, outer hinge plates, crural bases directed ventrally and low septum.

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# First finding of an articulated actinopterygian skeleton from the Upper Devonian of Siberia and a reappraisal of the family Moythomasiidae Kazantseva, 1971 (Osteichthyes)

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**Abstract.** *Krasnoyarchthys jesseni* gen. et sp. nov. is described from the Upper Devonian (Famennian) of Western Siberia. It is the first finding of a Devonian actinopterygian in Siberia. This new genus is closely related to *Moythomasia*, *Mimia* and *Kentuckia*, but differs from those genera in the relative position of the fins, longer pelvic fin base and other dermal roof bones and scales characters in combination. The family Moythomasiidae with the above-mentioned genera and possibly *Orvikuina* is re-diagnosed and compared.

**Key words:** Actinopterygii, Moythomasiidae, systematics, Upper Devonian, Western Siberia.

## Introduction

Actinopterygian remains from the Devonian are known usually by isolated scales and disarticulated bones, or by highly incomplete fragments of skeletons; more or less completely articulated specimens are rare. Such remains are known from Western Europe and the Baltic region of Central Europe, Spitzbergen, Afghanistan, North and South America and Australia (Agassiz, 1833–1844; Woodward and White, 1926; Gross, 1942, 1950, 1953; Lehman, 1947; Casier, 1952, 1954; Gardiner, 1963; Berg *et al.*, 1964; Jessen, 1968; Schultze, 1968; Gardiner and Bartram, 1977; Pearson and Westoll, 1979; Blicek *et al.*, 1982; Janvier and De Melo, 1987; Long, 1988; Gagnier *et al.*, 1989; Taverne, 1997). Only isolated scales identified as cf. *Moythomasia* sp. were found in Afghanistan (Blicek *et al.*, 1982) and no more or less completely articulated specimens of Devonian actinopterygians were described from Asia. However, a collection of the Paleontological Institute (PIN) in Moscow includes a single nearly complete skeleton from the Upper Devonian deposits of the Krasnoyarski Krai in Western Siberia. This specimen shares many similarities with the genus *Moythomasia* Gross but differs from the latter in several other respects (see below). In the present paper it is described as a new genus and species, *Krasnoyarchthys jesseni*. The family Moythomasiidae Kazantseva, 1971 is reappraised as a consequence of the description of the new

taxon.

## Notes on geography and stratigraphy

The fossil site is situated 150 km westward from Krasnoyarsk close to Nazarovo City in the southwestern part of the Krasnoyarski Krai (Figure 1). In an abandoned quarry near the Atshinsk-Abakan railroad, brown sandstones are exposed interrupted by calcareous alveolites with rare concretions. These layers belong to the Famennian Stage (Sidorenko, 1964). The specimen was found in a concretion.

## Systematic paleontology

Order Cheirolepiformes  
(sensu Kazantseva-Selezneva, 1977)  
Family Moythomasiidae Kazantseva, 1971

*Emended diagnosis.* — Relatively small fishes with fusiform body. Frontal bones as long as or 1.7 times longer than parietals. Both intertemporal and supratemporal present [intertemporal is not documented in *Kentuckia*, however, it might be present according to its reconstruction (Rayner, 1951, p. 56)]. Supratemporal not contacting frontal. Antorbital and single supraorbito-infraorbital present. Postorbital portion of maxillary well

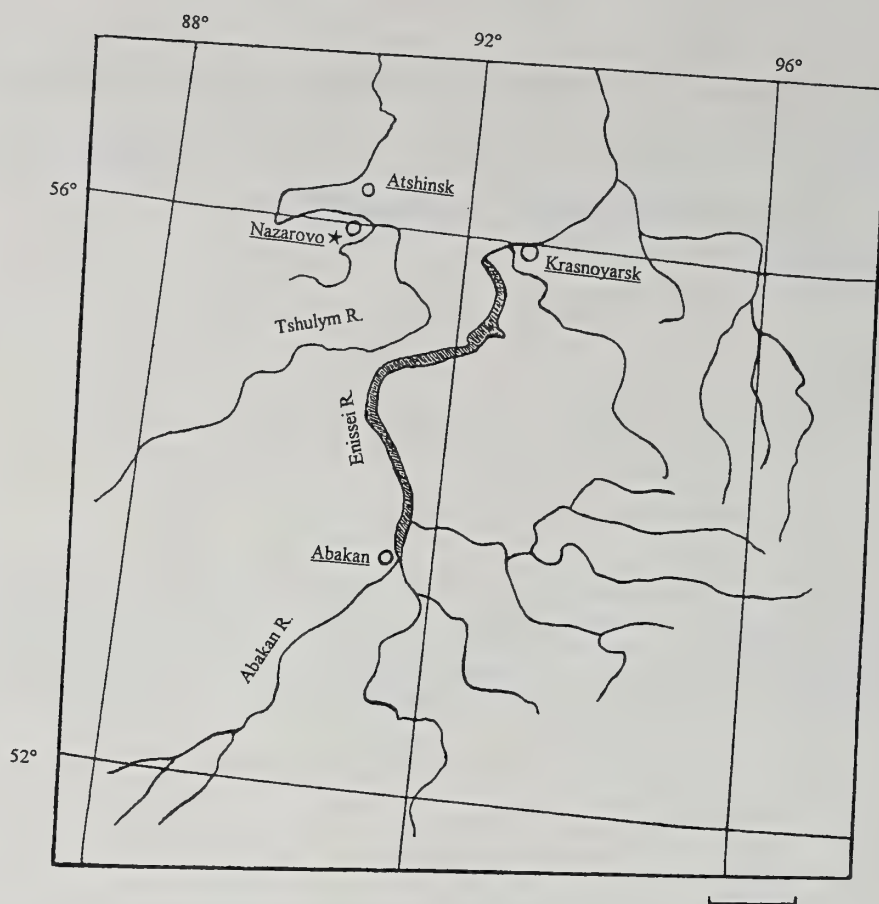


Figure 1. Map of a section of Western Siberia illustrating the location of the fossil site (★). Scale bar 75 km.

developed. Mandibular suspension oblique. Both dermohyal and epipreopercle present, completely separating opercle and preopercle. Preopercle with two branches. Opercle larger than subopercle. Skull roofing bones ornamented with longitudinal ridges of ganoine. All fins with minute fringing fulcra and with rays articulated and distally bifurcating. Dorsal and anal fins completely or partially opposite to one another; anal fin originating on the same level as the dorsal fin origin or behind it. Pelvic fin base shorter than anal fin base. Caudal fin heterocercal. Dorsal and ventral ridge scutes present. Scales ornamented with diagonal ridges which end on the posterior scale margins as a series of serrations; all body scales with peg-and-socket articulations.

*Included genera.*—*Moythomasia* Gross, 1950 (Middle-Upper Devonian, Western and Central Europe, ?Afghanistan, Western Australia); *Kentuckia* Rayner 1951 (Lower Carboniferous, USA); *Mimia* Gardiner and Bartram 1977 (Upper Devonian, Western Australia); *Krasnoyarichthys*, gen. nov. (Upper Devonian, Western Siberia); possibly also *Orvikuina* Gross, 1953 (Middle Devonian, Central Europe), which is known only by isolated scales.

### *Krasnoyarichthys* gen. nov.

*Type species.*—*Krasnoyarichthys jesseni*, sp. nov.; monotypic genus.

*Etymology.*—From the Krasnoyarsky Krai, and *-ichthys* (Greek), fish; masculine.

*Diagnosis.*—Same as that of the type species.

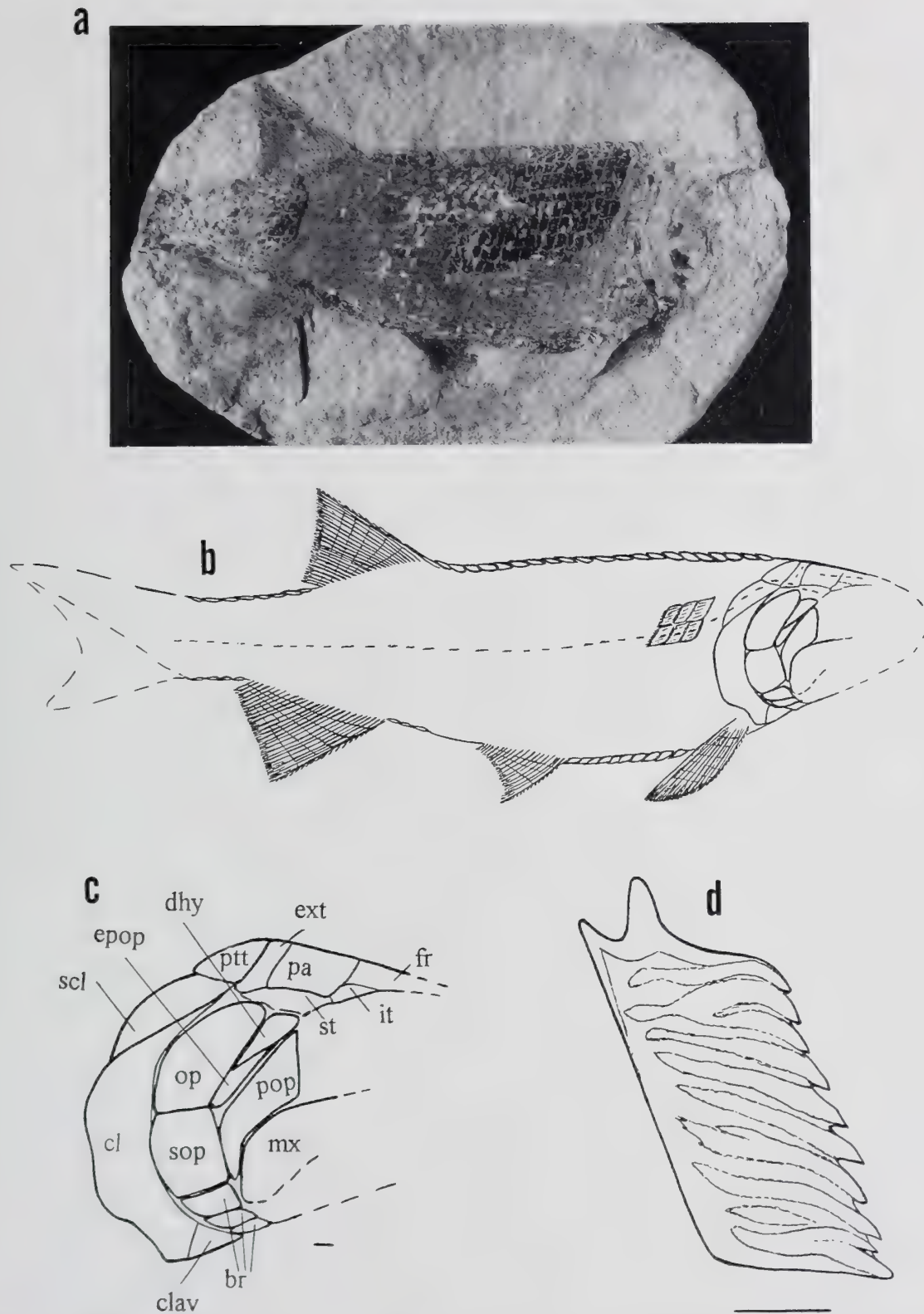
### *Krasnoyarichthys jesseni* sp. nov.

*Holotype.*—PIN, nr. 4890-1, nearly complete skeleton lacking snout, anterior parts of the skull roof and of the cheek, and caudal fin, with poorly preserved cephalic sensory canals and limits of scales on the caudal peduncle; single plate (Figure 2a); Western Siberia, Krasnoyarski Krai, vicinity of Nazarovo City, Preobrazhensky Village, quarry near railroad; Upper Devonian (Famennian). Species is known only by the holotype.

*Ethymology.*—Species named in honour of Hans Jessen for his great contribution to palaeoichthyology.

*Diagnosis.*—Relatively small fishes reaching a total length of about 10 cm. Maximum body depth contained





**Figure 2.** *Krasnoyarchthys jesseni* gen. et sp. nov., Upper Devonian (Famennian) of Krasnoyarski Krai (Siberia). **a.** Holotype, PIN, nr. 4890-1 (natural size). **b.** Reconstruction of the lateral view. **c.** Reconstruction of the postorbital part of the skull and of the pectoral girdle (as the cephalic sensory canals are poorly preserved they are omitted in figure). **d.** Isolated scale from left side of body. Scale bars 1 mm. Abbreviations: br, branchiostegal rays; cl, cleithrum; clav, clavicle; dhy, dermohyal; epop, epipreopercle; ext, extrascapular; fr, frontal; it, intertemporal; mx, maxillary; op, opercle; pa, parietal; pop, preopercle; ptt, posttemporal; scl, supracleithrum; sop, subopercle; st, supratemporal.

approximately 3.5 times in the total length. Extrascapular single on each side of skull, two times larger than long. Postorbital portion of maxillary deep. Opercle 1.5 times deeper than long. Subopercle 1.5 times smaller than opercle. Pelvic fin originating equidistantly from the pectoral and anal fin origins; pelvic base only 1.5 times shorter than anal fin base. Dorsal fin origin in front of that of anal fin; posterior edge of anal fin noticeably behind that of dorsal fin. Approximate numbers of fin-rays: dorsal 40, anal 40, pelvic 30, pectoral 30. Roofing bone ornament consisting of coarse longitudinal and diagonal ridges of ganoine. Scales rhomboidal, ornamented by up to 10 diagonal ridges which end on posterior scale margins as series of serrations. Middle trunk scales approximately twice, or less, deeper than long. Dorsal and ventral ridge scutes weakly developed.

**Description** (Figure 2).—Besides the characters given in the diagnosis there are several additional features. The estimated standard length of the holotype is approximately 100 mm. Measurements in mm: length from the posterior border of the cleithrum to the caudal base 76, length from the posterior border of the cleithrum to the dorsal fin origin 41, the same length to the anal fin origin 46, the same length to the pelvic fin origin 24, distance between the pectoral and pelvic fin origins 26, distance between the pelvic and anal fin origins 26, maximum body depth 32, caudal peduncle depth 8, dorsal fin base length 16, anal fin base length 16, pelvic base length 11, dorsal fin height 20, anal fin height 18, pelvic fin height 9, pectoral fin height 11. The transverse rows of scales on the body are approximately 50 in number. There are 16 longitudinal rows of scales on the body. The dorsal ridge scutes are continuous from the occiput to the dorsal fin origin, and between the dorsal and caudal fins. The ventral ridge scutes are between pectoral and pelvic fins, and between anal and caudal fins; at least three slightly enlarged ventral scales are present before anal fin origin.

### Discussion

Based on its similar body form, position of the fins, cranial roofing bones and structure of the scales *Krasnoyarichthys* undoubtedly belongs to the family Moythomasiidae. However, the new genus differs from both *Moythomasia* and *Mimia* in the relative position of the dorsal and anal fins (dorsal fin origin and ending in front of those of anal fin vs. dorsal and anal fins opposite one another in the compared genera) and in the slightly longer pelvic fins (1.5 times in the length of the anal fin base vs. twice in the compared genera). It further differs from *Moythomasia* in the presence of a single extrascapular on each side of the skull (vs. two in *Moythomasia*), which is noticeably larger than long (the extrascapulars are approxi-

mately as large as long in *Moythomasia*). *Krasnoyarichthys* is distinguished from *Mimia* in the middle trunk scales being no more than twice times deeper than long (vs. 3–4 times deeper than long in *Mimia*) and in the much less prominent ridge scutes. The new genus differs from *Kentuckia*, which is known only by the skull, in the opercle 1.5 times (vs. 2.5 times) deeper than long and 1.5 times (vs. twice) larger than the subopercle, and in the deep postorbital portion of the maxillary. The new genus is distinct from *Orvikuina*, which is known only by isolated scales, in having scales deeper than long (vs. much longer than deep), bearing up to 10 serrations (vs. 2–3 in *Orvikuina*).

The family Moythomasiidae is neglected in the literature. The genus *Moythomasia* together with *Kentuckia* Rayner and *Stegotrachelus* Woodward and White were placed by Gardiner (1963) in the family Stegotrachelidae. Later, Gardiner and Bartram (1977) added the genus *Mimia* to this family. However, the subsequent reconstruction of *Moythomasia* published by Jessen (1968) shows numerous distinctions between the latter and *Stegotrachelus*. Kazantseva (1971) indicated the principal differences between *Stegotrachelus* and *Moythomasia* were in the structure of the bones of the cheek region (both dermohyal and epipreopercle are absent in *Stegotrachelus*) and transferred *Moythomasia* and *Kentuckia* to another family, the Moythomasiidae. Unfortunately, this decision was never discussed by other authors (Gardiner, 1984; Gardiner and Schaeffer, 1989; Taverne, 1997).

In their phylogenetic analysis of the basal actinopterygians, Gardiner and Schaeffer (1989) placed *Mimia* and *Tegeolepis* into a «*Mimia* group», and *Moythomasia*, *Howqualepis* and *Stegotrachelus* into a «*Moythomasia* group»; the «*Mimia* group» was considered as a sister taxon for the «*Moythomasia* group» plus other actinopterygians excluding *Cheirolepis* and the polypterids. Unfortunately, this analysis is based on many characters not preserved in numerous paleoniscoid groups known to date (i.e. characters of the neurocranium, pectoral and pelvic girdles, axial skeleton, etc.), and their phylogenetic significance therefore needs further elucidation. In our opinion, the structure of the dermal skull bones provides the most important data for elucidation of paleoniscoid relationships, because they are always preserved in fossils and indicate the different evolutionary trends (Kazantseva-Selezneva, 1981). The only dermal bone character mentioned by Gardiner and Schaeffer (1989) as common to *Stegotrachelus* and *Moythomasia* is the absence of a true dermopterotic. The *Cheirolepis*, *Mimia* and *Moythomasia* groups of Gardiner and Schaeffer (1989) have no dermopterotic but two bones (intertemporal and supratemporal) in this region of the skull. However, in Gardiner's (1963: 296, fig. 12) reconstruction of the



*Stegotrachelus* skull the intertemporal is not figured. The other dermal skull characters of *Stegotrachelus* [absence of accessory opercular bones, long supratemporal (or dermopterotic) contacting frontal, small parietals, very narrow extrascapulars, numerous suborbitals] clearly distinguish the latter from the other members of the above-mentioned groups. According to Kazantseva-Selezneva (1981), the family Moythomasiidae seems to be closely related to the Cheirolepididae and Cosmoptychiidae rather than to the Stegotrachelidae. On the other hand, Taverne (1997) considered all the Devonian genera, *Cheirolepis* and *Dialipina* excluded, as the sister group of «polypteriforms». This opinion is doubtful judging from the close relationships between the Polypteridae and the peculiar Triassic Scanilepiformes (Sytchevskaya, 1999), and Lund's (2000) cladistic analysis of the polypteriforms which has specified sister relationships between the polypterids plus guildayichthyiforms and the platysomiforms.

According to Kazantseva (1971, 1974a, 1974b, 1977, 1981), the presence or absence of the dermohyal and epipreopercle is highly significant for the higher classification of the paleoniscoid fishes and indicates different types of breathing. Kazantseva-Selezneva (1977, 1981) divided the order Palaeonisciformes into three separate orders (Cheirolepiformes, Elonichthyiformes and Palaeonisciformes s. str.), of which both the dermohyal and epipreopercle are present only in the Cheirolepiformes. Among the Cheirolepiformes, the structure of the cranial roofing bones of the Moythomasiidae is similar to that in the Cheirolepididae. Both families have a single supraorbito-infraorbital, large parietals, the supratemporal lacking contact with the frontal bone, and the preopercle and opercle completely separated by the dermohyal and epipreopercle. However, the Cheirolepididae sharply differ from the Moythomasiidae in the structure of their scales, which are minute, square, not overlapping, with an internal boss, and quite similar to those of the acanthodians in the Cheirolepididae (contrary to the typical palaeoniscoid scales of the Moythomasiidae). The other distinctions include the presence of a separate antorbital in the Moythomasiidae [vs. completely fused with the premaxillary into the rostro-premaxillo-antorbital bone (Gardiner, 1963; Pearson and Westoll, 1979)], the anal fin origin opposite the dorsal fin origin or just behind it in the Moythomasiidae (vs. in advance of the dorsal fin origin in the Cheirolepididae), the pelvic base shorter than the anal base, and the ridge scutes present in the Moythomasiidae (in contrast to the reverse conditions in the Cheirolepididae) and the body form less elongate in the Moythomasiidae.

In our opinion, the family Moythomasiidae is valid and closely related to the Cheirolepididae. Such cranial characters as long parietals, presence of intertemporals,

supratemporals lacking contact with frontal bones, single infraorbito-suborbital, and dermohyal and epipreopercle completely separating the preopercle from the opercle characterising both these families seem to be primitive, according to the undoubted position of *Cheirolepis* as the most primitive actinopterygian (Berg *et al.*, 1964; Pearson and Westoll, 1979; Patterson, 1982; Lauder and Liem, 1983; Gardiner and Schaeffer, 1989; etc.). The orbit relatively larger with regard to the overall body size, the shorter body, the short-based pelvic fins, the presence of peg-and-socket scale articulations on the body scales and ridge scutes on the body contours indicate the advanced status of the Moythomasiidae. The peculiar Australian genus *Howqualepis* has small orbits, a long body, and long-based pelvic fins, and it lacks dorsal and ventral ridge scutes, which establishes its similarity to *Cheirolepis*; however, the supratemporal has contact with the frontal and the parietals are two times shorter than the frontals in *Howqualepis* (Long, 1988). All these characters undoubtedly exclude *Howqualepis* from the Moythomasiidae. The other Devonian genera (*Dialipina* and *Ligulalepis*, which are known only by isolated scales; *Osorioichthys* and *Tegeolepis*) sharply differ from the Moythomasiidae in the cranial and scale characters and the two latter belong to other families (Osorioichthyidae and Tegeolepididae, respectively) (Schultze, 1968; Gardiner, 1963, 1967; Kazantseva-Selezneva, 1977, 1981).

### Conclusion

*Krasnoyarchichthys jesseni* gen. et sp. nov. from the Upper Devonian (Famennian) of Western Siberia belongs to the family Moythomasiidae, and differs from the other members of this family in the following combination of characters: single extrascapular on each side of the skull, which is noticeably larger than long; deep postorbital portion of maxillary; opercle 1.5 times deeper than long and 1.5 times larger than the subopercle; dorsal fin origin in front of that of anal fin; posterior edge of anal fin noticeably behind that of the dorsal fin; pelvic fin base 1.5 times in the anal fin base length, and middle trunk scales no more than twice deeper than long. The family Moythomasiidae presently is recognized as distinct and closely related to the Cheirolepididae, on the basis of their similar cranial roofing bone characters. However, the moythomasiids seem to be more advanced than the cheirolepidids judging from their relatively larger orbit with regard to the overall body size, shorter body, short-based pelvic fins, the presence of peg-and-socket scale articulations on the body scales and ridge scutes on the body contours.

The moythomasiids and other Devonian actinopterygians are recorded in marine sediments only (Jessen, 1968; Schultze, 1968; Gardiner, 1984; Janvier and De Melo,

1987; etc.), and Sidorenko (1964) noted a marine origin for the deposits, in which the holotype of *Krasnoyarchthys* subsequently was found. This taxon is the first finding of the Moythomasiidae in Siberia. Further investigations of the Preobrazhensky fossil site are needed since they have special interest for the morphology, taxonomy and paleobiogeography of Devonian actinopterygians.

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## Errata

In the article by Takashi Matsubara (*Paleontological Research*, Vol. 6, No. 2, pp. 127–145), the following corrections should be made:

page	table/column	line	read	for
130	Table 1	9	<i>Acila (Truncacila) cf. nagaoi</i>	<i>Acila (Truncacila) cf. nagaoi</i>
130	Table 1	11	<i>Glycymeris (Glycymeris) sp.</i>	<i>Glycymeris (glycymeris) sp.</i>
130	Table 1	15	<i>Chlamys (Leochlamys) namigataensis</i>	<i>Chlamys (leochlamys) namigataensis</i>
130	Table 1	16	<i>Crassostrea sp.</i>	<i>Crassastrea sp.</i>
130	Table 1	17	Lucinidae gen. et sp. indet.	Luchinidae gen. et sp. indet.
130	Table 1	18	<i>Cyclocardia sp.</i>	<i>Cyclocardin sp.</i>
130	Table 1	20	<i>Megangulus maximus</i> (Nagao)	<i>Megangulus maximus</i> (Nagano)
141	Left	44	[delete]	Fo
141	Left	45	Formation	rmation
142	Left	4	Activities, Hyogo/Himeji Institute	Activities, Hyogo Himeji Institute
143	Right	7	<i>Editio duodecima</i>	<i>Editio decima</i>
144	Right	21	<i>siciliale</i>	<i>Siciliale</i>
144	Right	23	<i>Tome 2</i>	Tom 2
144	Right	30	<i>Pars secunda</i> , viii+199 p.	<i>Pars Secunda</i> , viii-199p.

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## 行 事 予 定

◎第152回例会は、2003年1月24日（金）～26日（日）に横浜国立大学教育人間科学部にて開催の予定です。1月24日（金）にシンポジウムとして「白亜紀海洋無酸素事件の解明：世話人 平野弘道・北里 洋・西 弘嗣」が、また1月25日（土）にシンポジウム「中・古生代微化石研究の現状と将来－テレーン解析後の使命－：世話人 指田勝男」が開催されます。なお、講演の申し込み締め切りは、2002年11月29日（金）です。講演申し込みの予稿集原稿送付の際には発表で使用する機器（液晶プロジェクター、OHP、スライドなど）の希望について明記して下さい。

◎2003年年会総会は、2003年6月下旬に静岡大学理学部で開催されます。シンポジウム「生物多様性を古生物学から考える：世話人 塚越 哲・北村晃寿・生形貴男」を開催予定です。講演の申し込み締め切りは2003年5月2日（金）の予定です。このほか、夜間小集会などの希望予定がありましたら、2002年12月初旬までに行事係までお知らせ下さい。

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### CONTENTS

- Rajeev Patnaik:** Enamel microstructure of some fossil and extant murid rodents of India ..... 239
- Yutaka Honda:** Paleobiogeographic significance of *Trominina hokkaidoensis* (Hayasaka and Uozumi) (Gastropoda: Buccinidae) from the basal part of the Tanami Formation (Oligocene) of the Kii Peninsula, southern Japan ..... 259
- Gengo Tanaka and Noriyuki Ikeya:** Migration and speciation of the *Loxoconcha japonica* species group (Ostracoda) in East Asia ..... 265
- Guang R. Shi, Shuzhong Shen and Jun-ichi Tazawa:** Middle Permian (Guadalupian) brachiopods from the Xiujimqinqi area, Inner Mongolia, northeast China, and their palaeobiogeographical and palaeogeographical significance ..... 285
- Neda Motchurova-Dekova, Michiko Saito and Kazuyoshi Endo:** The Recent rhynchonellide brachiopod *Parasphenarina cavernicola* gen. et sp. nov. from the submarine caves of Okinawa, Japan ..... 299
- Artém M. Prokofiev:** First finding of an articulated actinopterygian skelton from the Upper Devonian of Siberia and a reappraisal of the family Moythomasiidae Kazantseva, 1971 (Osteichthyes) ..... 321
- Errata:** Article by Takashi Matsubara in Vol. 6, No. 2 ..... 329



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Cover: Typical Pleistocene fossils from the Japanese Islands. Front cover: *Sinomegaceros yabei* (Shikama). Back cover: *Paliurus nipponicum* Miki, *Mizuhopecten tokyoensis* (Tokunaga), *Neodenticula seminae* (Simonsen and Kanaya) Akiba and Yanagisawa and *Emiliana huxleyi* (Lohmann) Hay and Mohler.

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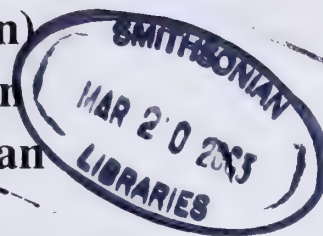
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# Lithology and foraminiferal fauna of allochthonous limestones (Changhsingian) in the upper part of the Toyoma Formation in the South Kitakami Belt, Northeast Japan



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**Abstract.** Allochthonous limestones less than 3 m thick are intercalated lenticularly within sandstones and mudstones of the upper part of the Upper Permian Toyoma Formation in the South Kitakami Belt. They are bedded and laminated, and have many thin interbeds of sandstone and mudstone. These limestones are narrowly distributed exclusively in the Kesennuma area, and largely differ from platform limestones of the Lower Permian Sakamotozawa and Middle Permian Kanokura formations, both widely distributed in the South Kitakami Belt, in their occurrence and extent. Thirty-two species of foraminifers, some of which are restricted to the Changhsingian, are discriminated in limestones, limestone conglomerates, and calcareous sandstones of the upper part of the Toyoma Formation. This foraminiferal fauna evidently belongs to the Tethyan province paleobiogeographically, and is characterized by dominant *Colaniella parva*, subordinate *Nanlingella cf. meridionalis*, and accessory *Palaeofusulina* sp. These three species are described herein.

**Key words:** allochthonous limestones, Changhsingian foraminifers, South Kitakami-Kurosegawa Old Land, upper part of Toyoma Formation

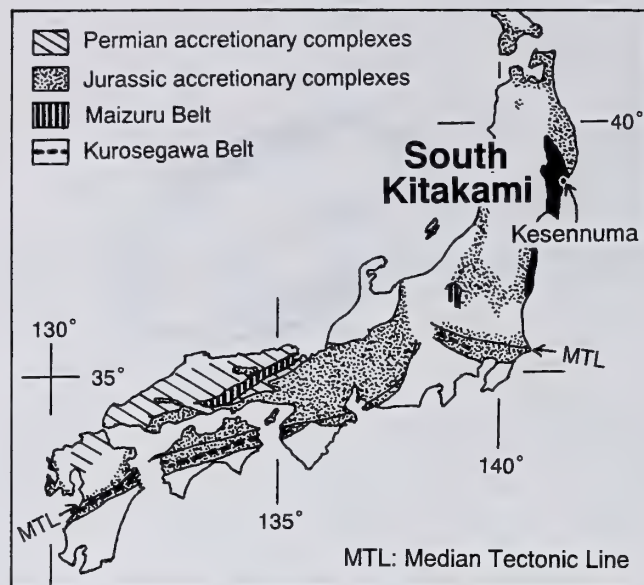
## Introduction

The South Kitakami Belt in Northeast Japan along with the Kurosegawa Belt in Southwest Japan is a distinct tectonic unit bounded by strike slip faults associated with serpentinite (Figure 1). Middle Silurian to Lower Cretaceous deposits rest on pre-Silurian granitic and metamorphic rocks in the South Kitakami Belt (Kawamura *et al.*, 1990) and in the Kurosegawa Belt (Yoshikura *et al.*, 1990). Paleozoic formations in these two belts are marked by shelf limestones containing terrigenous deposits and terrestrial plant fossils, which are absent in the pre-Cretaceous accretionary complexes of Japan.

The Permian of the South Kitakami Belt is subdivided into three units: Lower Permian Sakamotozawa Formation, Middle Permian Kanokura Formation, and Upper Permian Toyoma Formation (Figure 2). The Sakamotozawa Formation is dominated by platform limestones and overlies unconformably the Upper Carboniferous (Bashkirian) Nagaiwa Formation. The Kanokura Formation is marked by Murgabian to Midian reef complexes and thick granitic conglomerate. Based on faunas, floras, and limestone

lithologies of the Sakamotozawa and Kanokura formations, the South Kitakami Belt is thought to have been deposited in the equatorial Tethys in proximity to South China (Kawamura and Machiyama, 1995; Ehiro, 1997; Kobayashi, 1999). On the other hand, Middle Permian brachiopod faunas of the South Kitakami Belt are thought to be allied to those of Northeast China, Inner Mongolia, and South Primorye, and are different from the typical Tethyan faunas (Tazawa, 1991, 1998). The Toyoma Formation is represented by dominant argillaceous rocks. Limestones are less than 3 m thick, restricted to the upper part of this formation in the Kesennuma area, and present a striking contrast to widespread Lower and Middle Permian limestones in the South Kitakami Belt.

Fusulinaceans and their biostratigraphic zonation in the Sakamotozawa and Kanokura formations (Figure 2) were studied by Kanmera and Mikami (1965), Choi (1970), and others. Details on foraminiferal faunas of the Toyoma Formation have remained uncertain except for the occurrence of *Colaniella* and *Lantschichites* described by Tazawa (1975) and some late Permian foraminifers listed by Ishii *et al.* (1975).



This paper describes and discusses the limestone lithology and Changhsingian foraminiferal fauna of the upper part of the Toyoma Formation in the Kesennuma area. The allochthonous origin of the limestones of this formation is demonstrated. Three species of foraminifers, *Colaniella parva*, *Nanligella* cf. *meridionalis*, and *Palaeofusulina* sp., are described among the 32 taxa distinguished. All the described and illustrated specimens are stored in the Museum of Nature and Human Activities, Sanda, Hyogo, Japan.

### Lithostratigraphy

The Toyoma Formation consists mostly of mudstone (Figure 2), and yields Late Permian ammonoids (Ehiro and

Figure 1. Index geotectonic map of the Japanese pre-Cretaceous showing the South Kitakami Belt (black) and the Kesennuma area.

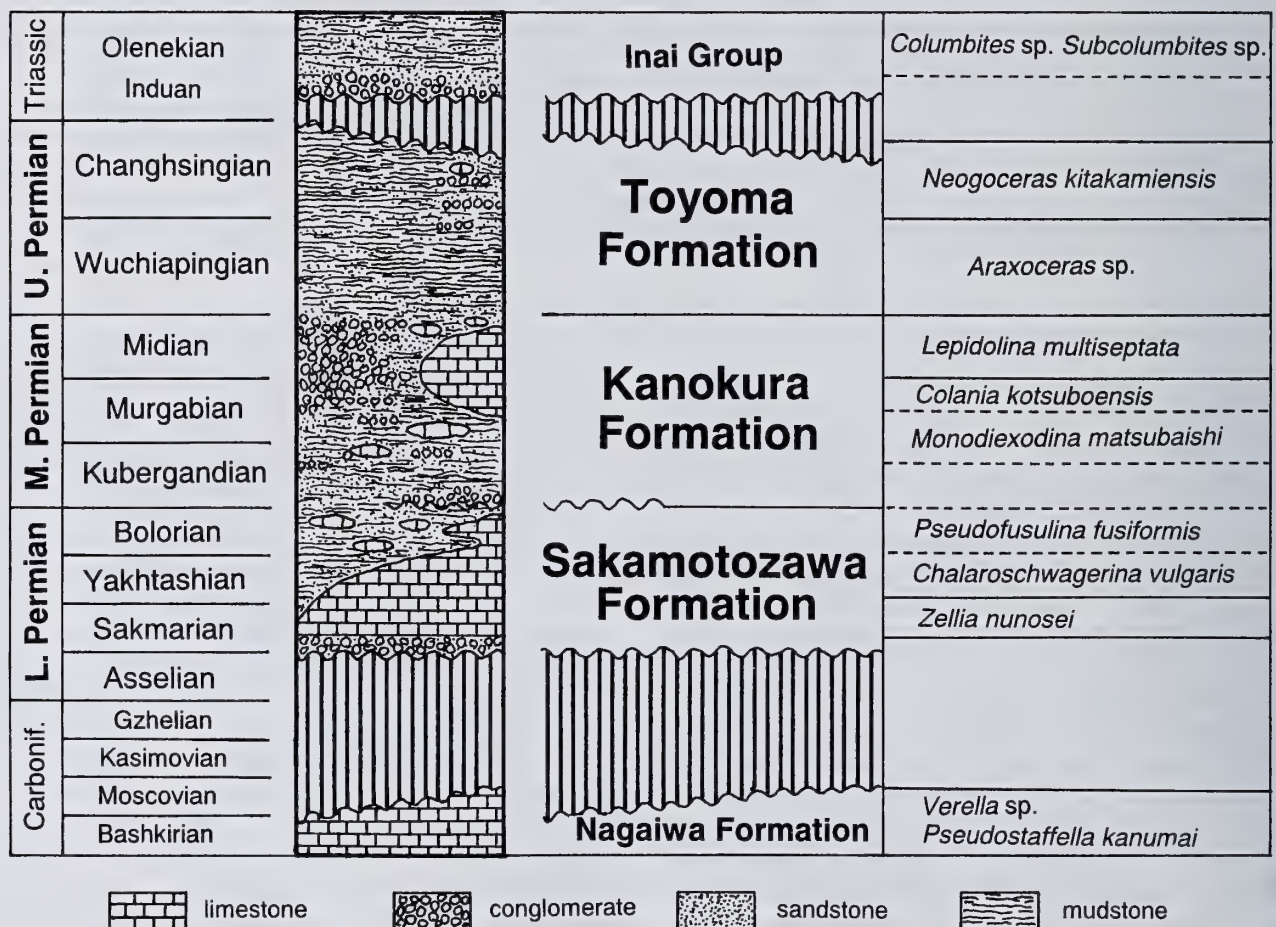
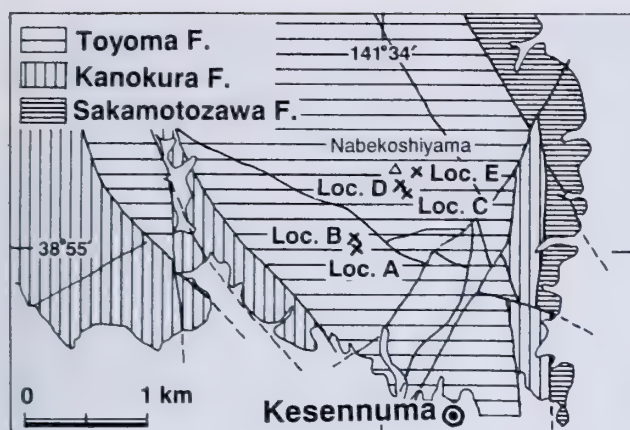


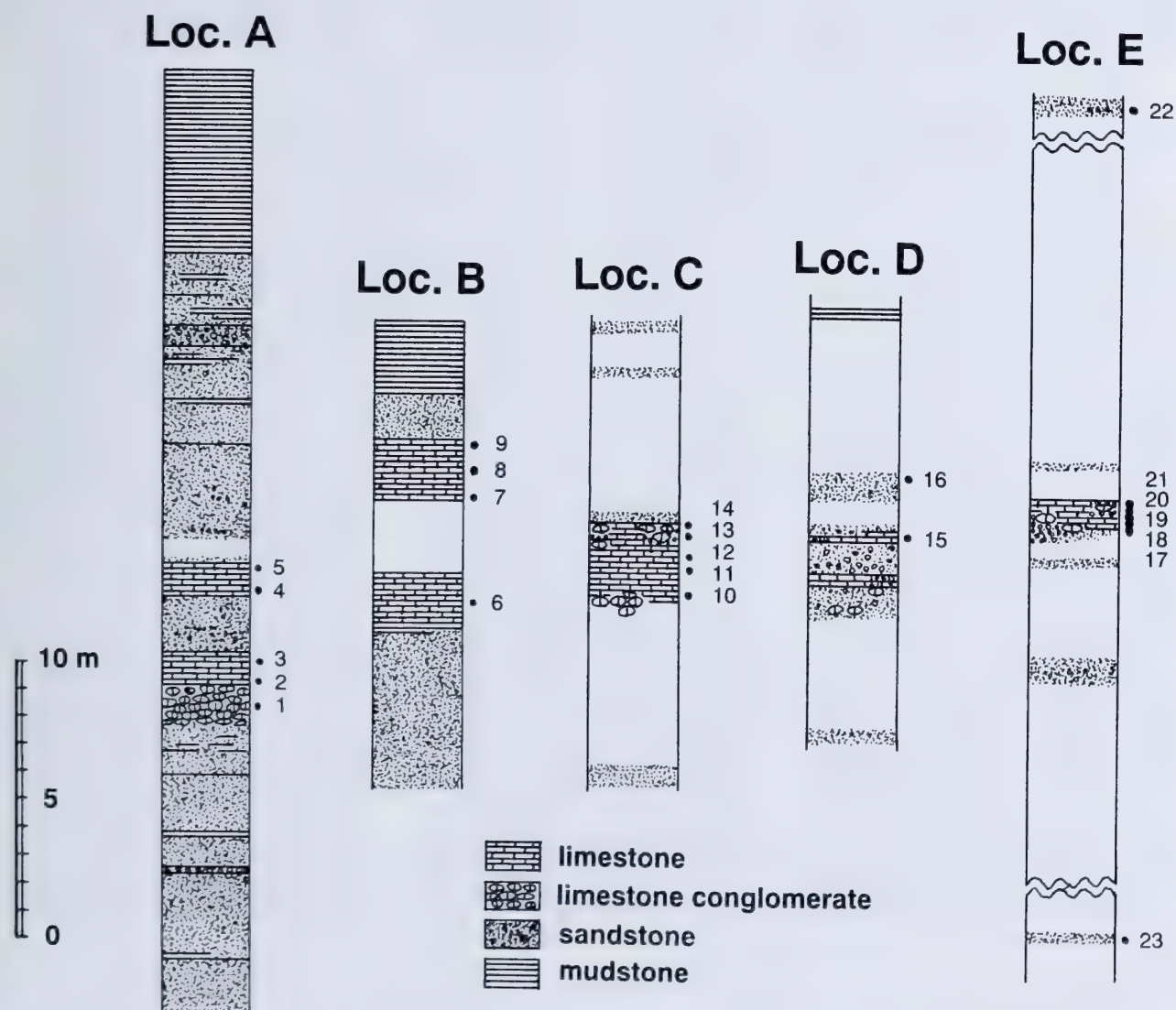
Figure 2. Schematic profile of the Permian of the South Kitakami Belt. Permian fusulinacean biostratigraphic subdivision is simplified based on Kanmera and Mikami (1965) and Choi (1970), and Permian ammonoids based on Ehiro (1987). Lower Permian Sakamotozawa Formation rests unconformably on the Upper Carboniferous Nagaiwa Formation.





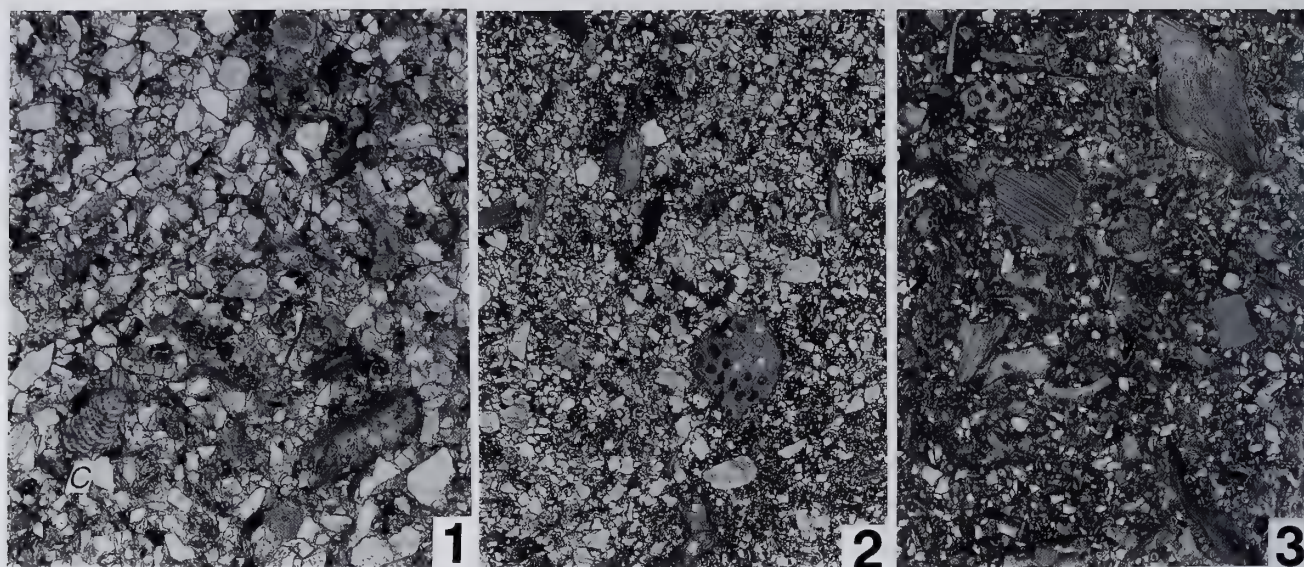
Bando, 1985; Ehiro, 1987), brachiopods (Tazawa, 1975, 1987), and others. In the Kesennuma area, the Toyoma Formation is divisible into lower and upper parts, and is partly intruded by dike rocks (Tazawa, 1976). The lower part consists of mudstone more than 600 m thick. The upper part is composed of a more than 500 m thickness of sandstone and mudstone interbedded with small amounts of thin conglomerate and limestone (Tazawa, 1975, 1976). Limestones and limestone conglomerates are lenticular, well-bedded, and have thin interbeds of sandstone and

**Figure 3.** Index geologic map showing locations of stratigraphic columns in Locs. A to E (shown in Figure 4) in the Kesennuma area, simplified based on Tazawa (1976).



**Figure 4.** Columnar sections of the upper part of the Toyoma Formation in Locs. A to E. Dots with number shows stratigraphic level of samples. Stratigraphically, sample 22 is about 40 m higher than sample 21, and sample 23 is about 65 m lower than sample 17.





**Figure 5.** Photomicrographs of sandstone and arenaceous limestone. 1, 2. Sandstone containing many lithic clasts and bioclasts. *Colaniella parva* (C) is found at the lower left corner in 1. 1. Loc. D-16,  $\times 10.8$ . 2. Loc. E-23,  $\times 6.6$ . 3. Arenaceous limestone containing many fossil fragments, and many detrital quartz and calcite grains within calcareous argillaceous matrix, Loc. E-19,  $\times 6.6$ .

mudstone. They are less traceable laterally, and sporadically distributed in five localities (Locs. A to E) north of Kesennuma (Figures 3, 4).

At Loc. A, a lenticular block surrounded by sandstone is exposed. It is 5.7 m thick, and consists of limestone conglomerate, lower limestone, sandstone, and upper limestone. The limestone conglomerate is 1.2 m thick, fossiliferous, and contains many subrounded pebbles to cobbles of limestone. This limestone conglomerate is overlain by the lower limestone, which has more than ten interbeds of mudstone and sandstone less than 5 mm thick. The lower limestone is 1.3 m thick, laminated, thinly-bedded, and contains well-sorted abundant fossils. Many fragments of brachiopods and crinoids are arranged parallel to the bedding plane of the lower limestone. The overlying coarse-to medium-grained sandstone is 2 m thick, highly calcareous, and partly porous due to the solution of calcareous materials and limestone clasts. Graded bedding is well developed in its basal part. The upper limestone overlying the sandstone is 1.2 m thick, well-bedded, and highly fossiliferous. It is lithologically similar to that of the lower limestone. The upper part of the upper limestone contains a few interbeds of mudstone 0.5 to 1 cm thick. The upper limestone is in contact with medium-to coarse-grained calcareous sandstone with many granules of limestone.

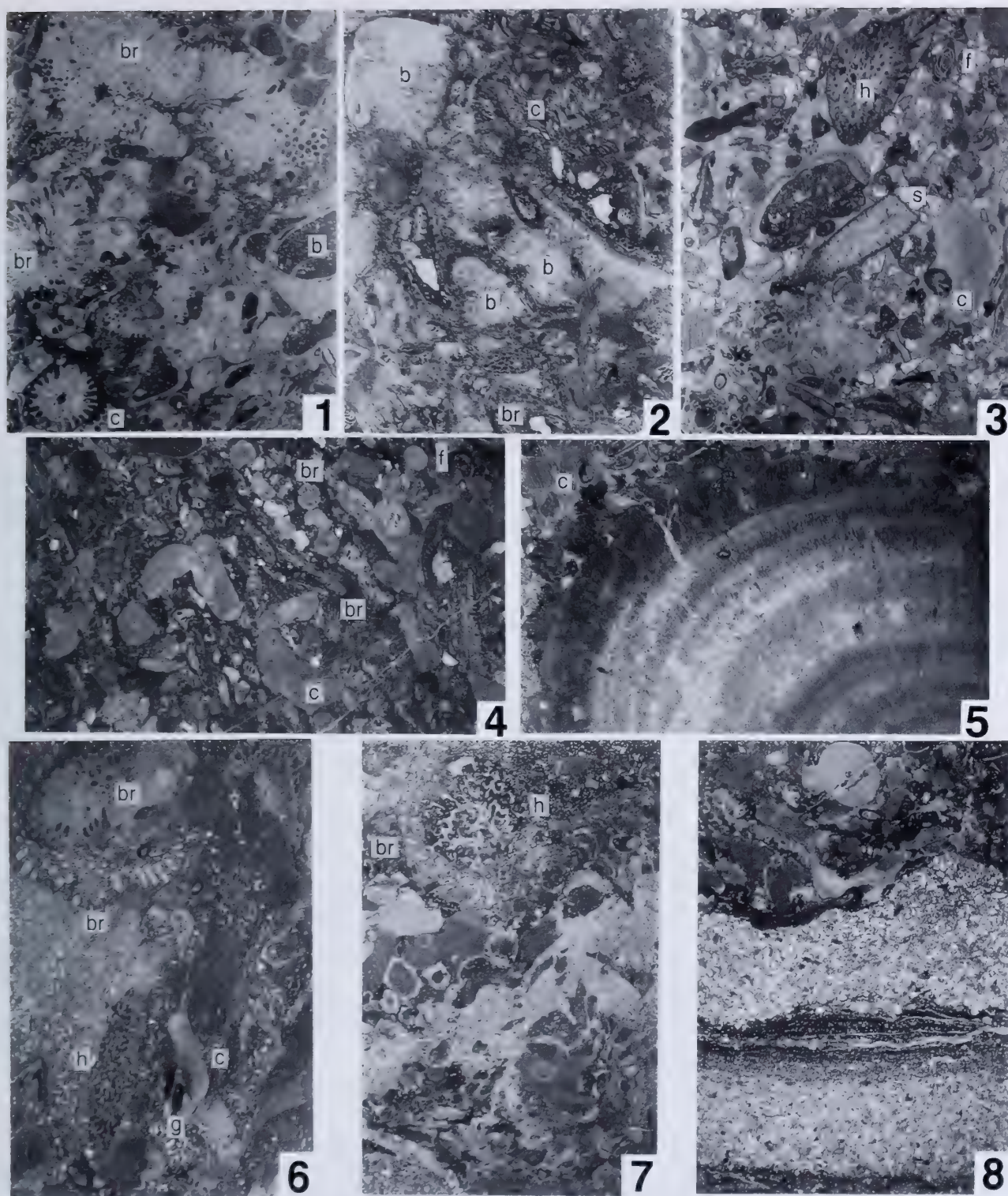
At Loc. B, limestones are developed in two horizons (Figure 4). The stratigraphic relationship between them is unknown. The lower limestone rests on the mudstone

without limestone conglomerate as found at Loc. A. The upper limestone is overlain by medium-to coarse-grained calcareous sandstone. Lower and upper limestones at Loc. B appear to be stratigraphically about 50 m higher than those at Loc. A. They are well-bedded, and contain abundant fossils and many thin interbeds of sandstone and mudstone like at Loc. A. These limestones at Locs. A and B have very similar lithologic characters and thicknesses.

Around Locs. C, D, and E, limestone and limestone conglomerate are more widely distributed than at Locs. A and B. They have in common thicknesses less than 3 m, are well-bedded, and have thin interbeds of calcareous sandstone and mudstone. Limestone conglomerate contains abundant fossil fragments, and ill-sorted granules to boulders of limestone, sandstone, and mudstone, all of which are packed within calcareous mudstone and sandstone. Many limestone granules and pebbles and fossil fragments are also found in sandstone (Figure 5.2). Bioclasts of foraminifers are contained in some of the sandstones (Figure 5.1).

The stratigraphic relationship of limestone and limestone conglomerate between Locs. A and B and Locs. C, D, and E is not confirmed exactly because of the sporadic occurrences of the limestone and a thick cover of soil and vegetation in this area. Besides these limestone conglomerates, a thin conglomerate with pebbles of granitic and porphyritic rocks without limestones is also found around Locs. C, D, and E.





**Figure 6.** Photomicrographs of limestone and limestone conglomerate. 1. Rudstone, Loc. A-1,  $\times 4$ . 2. Skeletal packstone/rudstone, Loc. A-3,  $\times 4$ . 3. Skeletal grainstone, Loc. E-18,  $\times 4$ . 4. Skeletal packstone, Loc. B-8,  $\times 4.5$ . 5. Stromatolite contained in limestone conglomerate, Loc. E-18,  $\times 5.1$ . 6, 7. Limestone conglomerate consisting of skeletal grains surrounded by highly calcareous argillaceous and arenaceous matrix, 6. Loc. E-21, 7. Loc. E-17, both  $\times 5.1$ . 8. Cobble of limestone (skeletal packstone) in contact with alternating beds of calcareous sandstone and mudstone showing lamination and graded bedding, Loc. E-17,  $\times 5.1$ . Skeletal grains contained show: bryozoans (br), crinoids (c), brachiopods (b), sponges (s), hydrozoa ? (h), green alga (g), and foraminifer (f).



### Lithologic characters and allochthonous origin of limestone

Limestones of the upper part of the Toyoma Formation are characterized by containing many detrital quartz grains and numerous and varied fossils, which in addition are small in size, intercalation of sandstone and mudstone, and well-developed stratification. Many fossils and detrital quartz grains are also contained in limestone granules to boulders of limestone conglomerates.

Limestones are composed of dominant skeletal packstone (Figure 6.2, 6.4). Rudstone (Figure 6.1) and skeletal grainstone (Figure 6.3) are also found. Some of these limestones contain discontinuous intercalations of sandstone and mudstone, and partly show a conglomeratic appearance. The limestone cobbles and pebbles in the conglomeratic part of the limestone at Loc. E are in contact with alternating beds of sandstone and mudstone with an undulated sharp boundary (Figure 6.8). Commonly found arenaceous limestone consists of fossils and lithic fragments packed with impure lime-mud (Figure 5.3). It is somewhat similar to calcareous sandstone containing many fossil fragments (Figure 5.1, 5.2). Fossils contained in these limestones are predominantly crinoids and bryozoans, with subordinate to accessory brachiopods, green algae, cyanobacteria, sponges (?), hydrozoans (?), foraminifers, and others.

Limestone conglomerate is composed of granules to boulders of fossiliferous limestone surrounded by highly calcareous mudstone and sandstone. Grain size, outline, and proportion of lithic fragments and skeletal grains against the surrounding mudstone and sandstone are variable in places (Figure 6.6, 6.7). Limestone granules to boulders also contain many detrital quartz grains, and are lithologically more diverse than the bedded limestone mentioned above. They consist of rudstone, skeletal packstone, skeletal grainstone, lime-wackestone, and lime-mudstone. The boundary between the limestone pebbles and surrounding calcareous mudstone is imprecise in some of the limestone conglomerate. Cyanobacteria, green algae, sponges, and hydrozoans (?) are commonly found in limestone conglomerates along with abundant crinoids and bryozoans. Stromatolites are sometimes included (Figure 6.5).

Occurrences and lithologies of lenticular limestone and conglomeratic limestone closely resemble those in the Upper Permian of the Kurosegawa Belt (Kobayashi, 2001b; unpublished data by the author) and the Maizuru Belt (unpublished data by the author). They are easily distinguishable from contemporaneous seamount limestones by having many detrital quartz grains and thin interbeds of sandstone and mudstone. Within the Japanese Upper Permian, limestone and limestone conglomerate of the upper part of the

Toyoma Formation are most similar to those of the Kuma Formation in the Kurosegawa Belt of west Kyushu. Fossil fragments contained in sandstones (Figure 5.1, 5.2), granules to boulders of limestones, and lenticular limestones are nearly the same age in the former. On the other hand, those of Yakhtashian to Bolorian, Midian, and Lopingian ages are confirmed in the latter (Kobayashi, 2001b). Although pre-Late Permian pebbles have not been found and the ages of the sandstone and mudstone are not exactly known, the lithology and occurrence of limestones and limestone conglomerates in the upper part of the Toyoma Formation suggest that they are allochthonous to the surrounding sandstone and mudstone, as well as the Kuma Formation. Kobayashi (2001b) concluded that limestones of the Kuma Formation had been redeposited in the setting of an active continental margin of the Kurosegawa Old Land in Late Permian time.

Abundant detrital quartz grains and fossils strongly evidence original limestone deposition on the shallow continental shelf in the upper part of the Toyoma Formation along with the Kuma Formation. The pre-Cretaceous formations in the South Kitakami and Kurosegawa belts are closely related stratigraphically and lithologically to each other, and the two belts are thought to have been isolated paleogeographically from the ancient Asian continent by the early Cretaceous amalgamation (Saito and Hashimoto, 1982; Kobayashi, 1999). Accordingly, all limestones of the upper part of the Toyoma Formation are considered to have been originally deposited on the shallow shelf referable to the South Kitakami-Kurosegawa Old Land as well as the Kuma Formation. Collapse and redeposition of limestone probably resulted from upheaval of the South Kitakami-Kurosegawa Old Land preceding the deposition of the Lower Triassic Inai Group resting unconformably on the Toyoma Formation. Remarkable differences in thickness, occurrence, and development of limestones between the Toyoma Formation and the underlying Sakamotozawa and Kanokura formations (Figure 2) are thought to be due to the allochthonous origin of these limestones in addition to the narrowing of the sedimentary basin of the Toyoma Formation.

### Foraminiferal fauna

Thirty-two species of foraminifers are distinguished in limestone, limestone conglomerate, and calcareous sandstone in the upper part of the Toyoma Formation in the Kesennuma area (Figures 7–9). Among them, *Colaniella parva* is the most representative in the Kesennuma fauna, and recognizable in almost all samples containing foraminifers. It is one of the most widespread species in the Upper Permian (Lopingian) of the Tethyan regions, ranging from the Mediterranean Sea regions to Japan and



	Loc. A					Loc. B				Loc. C					Loc. D		Loc. E							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
<i>Ammodiscus</i> sp.												x												
<i>Glomospira</i> ? sp.							x					?												
<i>Eolasiiodiscus</i> spp.						x	x													x				
<i>Lunucammina</i> cf. <i>palmata</i> (Wang)		x																		x	x			
<i>Colaniella parva</i> (Colani)	x	x	x	x	?	x	x	x	?	x	x	x	x	?	x	x	x	x	x	x	x	x	x	x
<i>Palaeotextulariidae</i> gen. and sp. indet.		x																		x				
<i>Dagmarita</i> ? sp.		x																						
<i>Tetrataxis</i> sp.								x																
<i>Abadehella</i> sp.		x					x	x										x		x				
<i>Reichelina changhsingensis</i> Sheng and Chang		x	x	x				x				x	x						x					
<i>Nanlingella</i> cf. <i>meridionalis</i> Rui and Sheng	x	x					x			x	?									x				
<i>Palaeofusulina</i> sp.				x																x				
<i>Nankinella</i> sp.		x																						
<i>Pseudovidalina</i> spp.																			x	x				
<i>Raphconilia</i> ? sp.																					x			
<i>Calcivertella</i> ? sp.																					x			
<i>Agathammina</i> cf. <i>pusilla</i> (Geinitz)	x						x					x												
<i>Agathammina</i> sp.	x								?			x												
<i>Agathammina</i> ? sp. A		x																		x				
<i>Agathammina</i> ? sp. B		x	x																					
<i>Hemigordius</i> sp. A							x					?												
<i>Hemigordius</i> sp. B							x																	
<i>Neodiscus</i> sp.																				x				
<i>Nikitinella</i> sp. A			x				x													x				
<i>Nikitinella</i> ? sp.			x			x	x						x							x				
<i>Kamurana</i> ? sp. A	x	x	x										x				x	?	x	x	x			
<i>Kamurana</i> ? sp. B		x	x																	x	x			
<i>Cryptoseptida</i> sp.							x												?	x				
<i>Geinitzina</i> spp.			x									x												
<i>Nodosinelloides</i> sp.										x											x			
<i>Pachyphloia</i> sp.	x						x																	
<i>Vervilleina</i> sp.		x		x			x													x				

Figure 7. Foraminifers distinguished in Locs. A to E.

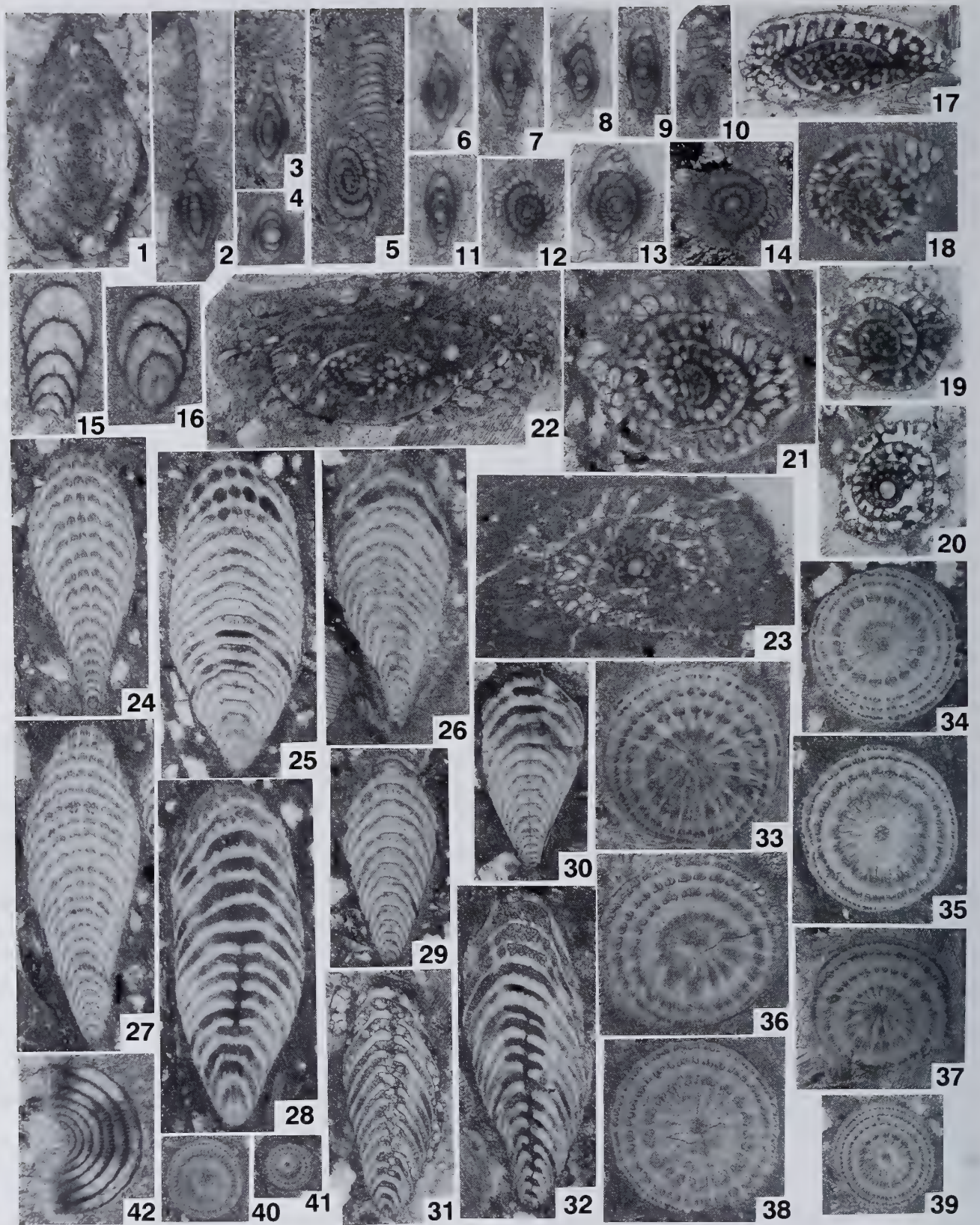
South Primorye (Jenny-Deshusses and Baud, 1989; Kobayashi, 1999). In Japan, *Colaniella parva* and allied species occur in the Changhsingian limestones of the Maizuru Group (Ishii *et al.*, 1975) and the Iwai-Kanyo area, southeastern part of the Kanto Mountains (Kobayashi, 1997), exclusive of the upper Toyoma Formation of the Kesennuma area, South Kitakami Belt. However, they have neither been reported from seamount limestones of Japan nor from any limestones of the Circum-Pacific regions.

*Nanlingella* cf. *meridionalis* is possibly identical with the original specimens of *N. meridionalis* described from the lower part of the Changhsingian of Guangdong and Hunan (Rui and Sheng, 1981). *Nanlingella simplex* and *Nanlingella* spp. are known from the Wuchiapingian limestone of Shaanxi (Rui *et al.*, 1984). According to Rui and Sheng (1981), *Nanlingella* probably appeared in the upper part of the *Codonofusiella* Zone (Wuchiapingian) and flourished in the lower and middle part of the *Palaeofusulina* Zone (Changhsingian). In Japan, *Nanlingella* cf. *meridionalis* in association with *Codonofusiella kwang-*

*siana*, *C. kueichowensis*, and others is known from the Wuchiapingian limestones of the Southern Chichibu Belt (Ota *et al.*, 2000; Kobayashi, 2001a). An incomplete specimen referred to as *Lantschichites* sp. by Tazawa (1975) from the upper Toyoma Formation of the Kesennuma area is probably referable to *Nanlingella*. Other schubertellids are very rare in the Kesennuma fauna. *Palaeofusulina* occurs exclusively in the Changhsingian, and is the most reliable foraminiferal genus for age determination of the uppermost Permian throughout the Tethyan regions (Rui and Sheng, 1981; Kobayashi, 1999).

Although a detailed age assignment is impossible, *Reichelina changhsingensis* and some genera such as *Abadehella* and *Dagmarita* found in the Kesennuma fauna are also common in the Upper Permian. Two forms possibly assignable to *Kamurana* and unidentified species referable to *Nikitinella* and *Pseudovidalina* are characteristic in some limestone samples. These milioliporid, baialinid, and involutinid foraminifers have not been reported from Japanese Permian limestones. Although they were not reported in Kobayashi (1997), they have been distinguished







in the Iwai-Kanyo fauna according to my reexamination of the fauna. They also occur in the Upper Permian limestones of the Maizuru Belt (unpublished data by the author). Staffellid fusulinaceans and *Tetrataxis* common in the Upper Permian are very rare, and endothyrids along with such genera as *Paraglobivalvulina*, *Robuloides*, and *Globivalvulina*, also common in the Changhsingian, are entirely lacking in the Kesennuma fauna.

A Changhsingian age for the present fauna is strongly suggested by the occurrences of *Colaniella parva*, *Nanlingella* cf. *meridionalis*, and *Palaeofusulina* sp. Paleobiogeographically, the Kesennuma fauna evidently belongs to the Tethyan province, and is allied to the Late Permian faunas known from the Kurosegawa and Maizuru Belts of Japan, South China, and Southeast Asia (Kobayashi, 1999). On the other hand, a Boreal-Tethyan mixed faunal component within South Kitakami, Maizuru, and Kurosegawa is suggested on the basis of geographical distribution of Permian brachiopods, especially of Middle Permian ones (Tazawa, 1987, 1998, 2000).

### Description of species

Family Colaniellidae Fursenko in Rauser-Chernousova and Fursenko, 1959

Genus *Colaniella* Likharev, 1939

*Colaniella parva* (Colani, 1924)

Figure 8.24-8.41

*Pyramis parva* Colani, 1924, p. 181, pl. 29, figs. 2, 4-14, 15a-15f, 16, 17, 19, 21, 24; Reichel, 1946, p. 544-547, Figs. 32-34, pl. 19, figs. 13, 14.

*Colaniella parva* (Colani). Tazawa, 1975, p. 632, 633, pl. 1, figs. 5-11; Kobayashi, 1997, pl. 2, figs. 1-27.

*Paracolaniella leei* Wang. Tazawa, 1975, p. 633, pl. 1, figs. 1-4.

**Material.**—More than 30 axial, slightly oblique axial, and transverse sections have been examined, of which 18 are illustrated.

**Description.**—Subfusiform test deviating to the terminal

part, about 0.8 mm in maximum width and more than 2 mm in maximum length. Initial chamber about 0.03 mm, followed by more than 20 chambers, dish-shaped in outline, strongly overlapping, gradually increasing in height and width. Chambers divided into chamberlets by 15 or more primary platy partitions extending along test axis. Each chamberlet subdivided by two or three secondary platy partitions. Secondary ones well developed even in early ontogenetic stage. Tertiary ones present partly at test margins. Wall finely perforate with fibrous structure.

**Discussion.**—Many specimens based on definitely oriented thin sections show variable appearances in biocharacters such as size and outline of test, apical angle, degree of tapering of test and overlapping of chambers, mode of incision of three kinds of platy partitions, and their ontogenetic development. The present materials are identical with the original specimens from Vietnam (Colani, 1924) based on variously oriented thin sections. They are also closely similar to the Iwai-Kanyo (Kobayashi, 1997) and other specimens. Collaniellids named *Colaniella parva* (Colani) and *Paracolaniella leei* Wang by Tazawa (1975) from the Kesennuma area are thought to be conspecific.

**Occurrence.**—Common to rare in Locs. A to E.

Family Schubertellidae Skinner, 1931

Genus *Nanlingella* Rui and Sheng, 1981

*Nanlingella* cf. *meridionalis* Rui and Sheng, 1981

Figure 8.17-8.21

*Lantschichites* sp., Tazawa, 1975, pl. 1, fig. 12.

*Nanlingella* cf. *meridionalis* Rui and Sheng. Ota *et al.*, 2000, fig. 6. 2-4; Kobayashi, 2001a, fig. 3. 14-18.

**Material.**—Tangential, sagittal, and three oblique sections illustrated herein, and others.

**Discussion.**—Although axial sections have not been obtained, the present materials are probably assignable to *Nanlingella*, and are compared with type species of this genus from South China. One sagittal section shown in

← **Figure 8.** 1. *Nankinella* sp., D2-022307a, Loc. A-2,  $\times 45$ . 2-14. *Reichelina changhsingensis* Sheng and Chang. 2. D2-022286a, Loc. A-2. 3. D2-022320, Loc. A-3. 4. D2-022364, Loc. B-7. 5. D2-022361a, Loc. B-7. 6. D2-022361a, Loc. B-7. 7. 022359a, Loc. B-7. 8. D2-022242a, Loc. C-12. 9. D2-022361b, Loc. B-7. 10. D2-022189, Loc. E-19. 11. D2-022324, Loc. A-3. 12. D2-022362, Loc. B-7. 13. D2-022359b, Loc. B-7. 14. D2-022349, Loc. B-8. All  $\times 60$ . 15, 16. *Lunucammia* cf. *palmata* (Wang). 15. D2-022198. 16. D2-022194a. Both Loc. E-20,  $\times 60$ . 17-21. *Nanlingella* cf. *meridionalis* Rui and Sheng. 17. D2-022296, Loc. A-2. 18. D2-022197a, Loc. E-20. 19. D2-022292, Loc. A-2. 20. D2-022286b, Loc. A-2. 21. D2-022205a, Loc. E-20. All  $\times 30$ . 22, 23. *Palaeofusulina* sp. 22. D2-022322a, Loc. A. 23. D2-022207a, Loc. E-20. Both  $\times 30$ . 24-41. *Colaniella parva* (Colani). 24. D2-022197b, Loc. E-20. 25. D2-022201a, Loc. E-20. 26. D2-022195A, Loc. E-20. 27. D2-022203a, Loc. E-20. 28. D2-022205b, Loc. E-20. 29. D2-022197, Loc. E-20. 30. D2-022389, Loc. B-6. 31. D2-022309, Loc. A-2. 32. D2-022390, Loc. B-6. 33. D2-022307b, Loc. A-2. 34. D2-022195b, Loc. E-20. 35. D2-022206, Loc. E-20. 36. D2-022211a, Loc. E-20. 37. D2-022280, Loc. A-2. 38. D2-022205c, Loc. E-20. 39. D2-022208a, Loc. E-20. 40. D2-022196, Loc. E-20. 41. D2-022200a, Loc. E-20. 24-32.  $\times 30$ , 33-41.  $\times 45$ . 42. *Eolasiodiscus* sp. D2-022372b, Loc. B-7,  $\times 60$ .



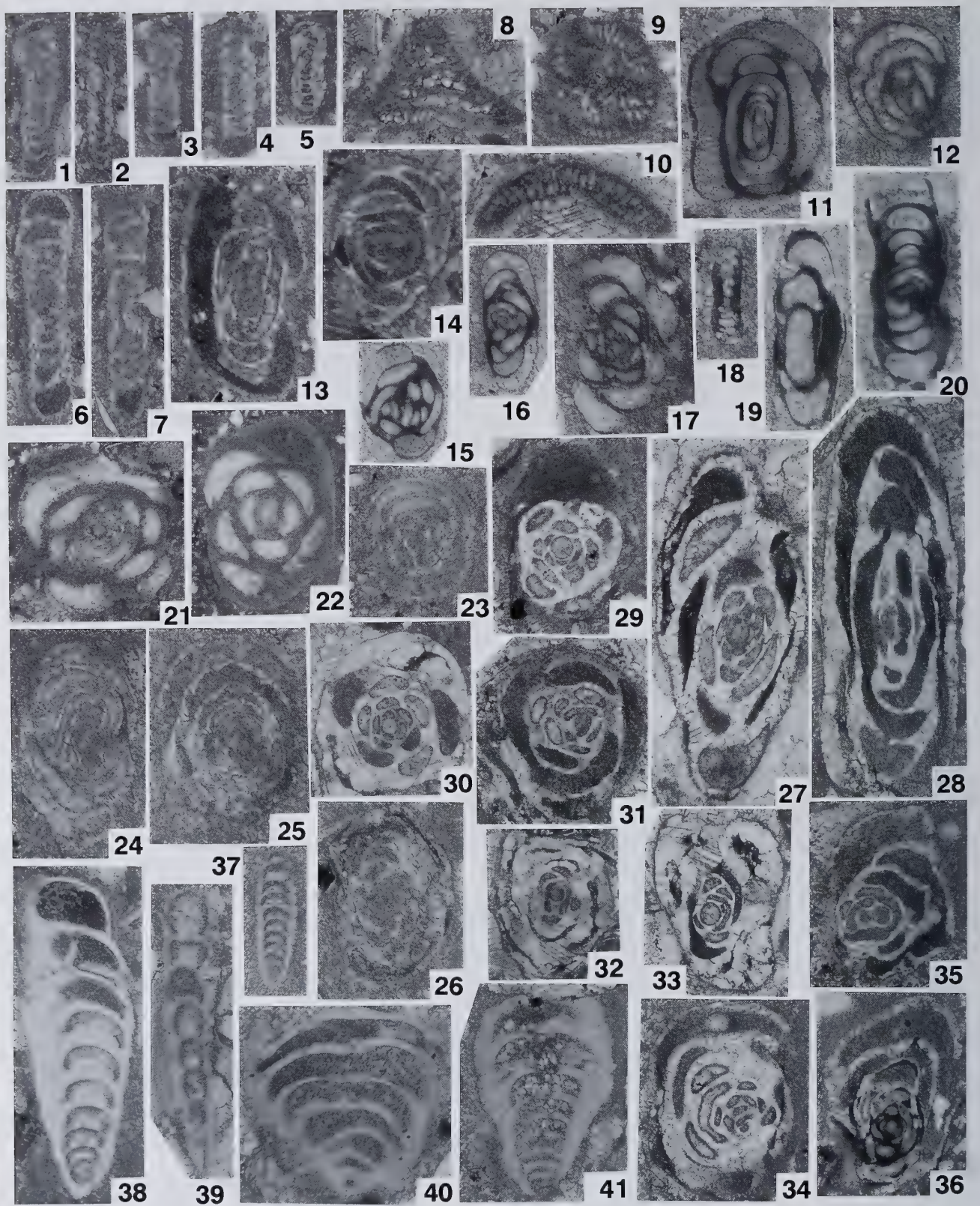




Figure 8.20 may be distinct from this species. An illustrated incomplete specimen, named *Lantschichites* sp. by Tazawa (1975) from the Kesennuma area possibly agrees with the present forms. *Nanlingella* cf. *meridionalis* of Ota *et al.* (2000) and Kobayashi (2001a) resembles the present materials in size of shell, septal fluting, and expansion of shell.

**Occurrence.**—Rare in Locs. A, B, C, and E, associated with *Palaeofusulina* sp. in Locs. A and E.

### Genus *Palaeofusulina* Deprat, 1912

#### *Palaeofusulina* sp.

Figure 8.22, 8.23

**Material.**—Tangential section and oblique section here illustrated, and others.

**Discussion.**—An oblique section illustrated in Figure 8.23 is thought to be more reasonably assignable to *Palaeofusulina* than to *Nanlingella* or other schubertellid genera based on lack of inner endothyroid volutions and proloculus size. A tangential section shown in Figure 8.22 is ascribed to the genus with reservation. Specific identification and further discussion are postponed until better oriented specimens are recovered. It is difficult to conclude that one incomplete specimen illustrated by Ota *et al.* (2000, fig. 6–5) is undoubtedly assignable to *Palaeofusulina*.

**Occurrence.**—Very rare in Locs. A and E.

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I thank Jun-ichi Tazawa and an anonymous reviewer, for their help in improving the manuscript, and John R. Groves for his comments on identification of some of the foraminifers. A part of this study was financially supported by a Grant-in Aid for Scientific Research (C) of the Japanese Ministry of Education, Science and Culture in 1994 (Project No. 05640521).

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← **Figure 9.** 1–5. *Pseudovidalina* spp. 1. D2–022191, Loc. E–20. 2. D2–022202a, Loc. E–20. 3. D2–022203b, Loc. E–20. 4. D2–022200b, Loc. E–20. 5. D2–022201b, Loc. E–20. All ×60. 6, 7. *Raphconilia* ? sp. 6. D2–022208b, Loc. E–20. 7. D2–022202b, Loc. E–20. Both ×60. 8–10. *Abadehella* sp. 8. D2–022353, Loc. B–8, ×45. 9. D2–022201c, Loc. E–20, ×30. 10. D2–022181, Loc. E–18, ×30. 11, 12. *Agathammina* cf. *pusilla* (Geinitz). 11. D2–022208b, Loc. E–20. 12. D2–022242b, Loc. C–12. Both ×60. 13, 14. *Agathammina* ? sp. A. 13. D2–022195c, Loc. E–20. 14. D2–022299, Loc. A–2. Both ×50. 15–17. *Agathammina* sp. 15. D2–022277a. 16. D2–022277b. 17. D2–02227901c. All Loc. A–1, ×60. 18. *Hemigordius* sp. A. D2–022359, Loc. B–7, ×80. 19, 20. *Hemigordius* sp. B. 19. D2–022361c. 20. D2–022373. Both Loc. B–7, ×60. 21, 22. *Neodiscus* sp. 21. D2–022200c. 22. D2–022207b. Both Loc. E–20, ×30. 23–26. *Nikitinella* spp. 23. D2–022194b, Loc. E–20. 24. D2–022203c, Loc. E–20. 25. D2–022328b, Loc. A–3. 26. D2–022358a, Loc. B–7. All ×60. 27, 28. *Agathammina* ? sp. B. 27. D2–022184, Loc. E–18. 28. D2–022312, Loc. A–3. Both ×30. 29–34. *Kamurana* ? sp. A. 29. D2–022313a, Loc. A–3. 30. D2–022297, Loc. A–2. 31. D2–022325, Loc. A–3. 32. D2–022316, Loc. A–3. 33. D2–022295, Loc. A–2. 34. D2–022313b, Loc. A–3. 35, 36. *Kamurana* ? sp. B. 35. D2–022317, Loc. A–3. 36. D2–022216, Loc. E–21. Both ×30. 37. *Nodosinelloides* sp. D2–022211b, Loc. E–20. ×60. 38. *Pachyphloia* sp. D2–022366b, Loc. B 7. ×60. 39. *Vervilleina* sp. D2–022293, Loc. A–2. ×60. 40, 41. *Cryptoseptida* sp. 40. D2–022366c. 41. D2–022358b. Both Loc. B–7, ×60.

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## A new coelacanth from the Early Cretaceous of Brazil (Sarcopterygii, Actinistia)

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**Abstract.** A new coelacanth fish of the genus *Mawsonia*, *M. brasiliensis* sp. nov. is described on the basis of a specimen from the Early Cretaceous Romualdo Member of the Santana Formation in the Araripe Plateau, Brazil. This is the third species of coelacanth from the Cretaceous of Brazil and the holotype is the first complete, articulated specimen of the genus. This new species differs from its congeners in the proportion of the cranium, gular plates and angular, and the position of the otic canal fossa. *M. brasiliensis* has thin cycloid scales without ornament (no tubercles or ridges). This new addition to the genus *Mawsonia* is significant in increasing understanding of the diversity of the suborder Latimeroidei in the early Cretaceous, which lineage continues to the Recent coelacanths of the genus *Latimeria*.

**Key words:** Araripe, Brazil, coelacanth, Early Cretaceous, *Mawsonia*, new species, Santana Formation

### Introduction

The Araripe Plateau, northeastern Brazil, is well known for its excellently preserved Early Cretaceous shallow marine and freshwater fossil assemblages (Maisey, 1991; Martill, 1993; Evans and Yabumoto, 1998). Two coelacanth species have been described from Cretaceous deposits in Brazil: *Mawsonia gigas* Woodward, 1907 from the Neocomian of Bahia, and *Axelrodichthys araripensis* Maisey, 1986 from the Romualdo Member of the Santana Formation. On the basis of an almost complete articulated specimen recovered from the Romualdo Member of the Santana Formation, Araripe Plateau, Brazil, a new species of the genus *Mawsonia* is proposed. An almost complete neurocranium and some other disarticulated head bones from the Romualdo Member that Maisey (1986) described as *M. cf. gigas* are referable to this new species. This new addition to the genus *Mawsonia* is significant in increasing understanding of the diversity of the suborder Latimeroidei in the early Cretaceous, which lineage continues to the Recent forms of coelacanths of the genus *Latimeria*. Figures were made using a camera lucida. Terminology of coelacanth bones follows Forey (1998) and of median fins follows Uyeno (1991).

### Systematic description

Order Coelacanthiformes Huxley, 1861  
Suborder Latimeroidei Schultze, 1993  
Family Mawsoniidae Schultze, 1993  
Genus *Mawsonia* Woodward, 1907

#### *Mawsonia brasiliensis* sp. nov.

Figures 1–4

*Mawsonia cf. gigas* Maisey, 1986, p. 3–13, figs. 1–11; Maisey, 1991, p. 317–323.

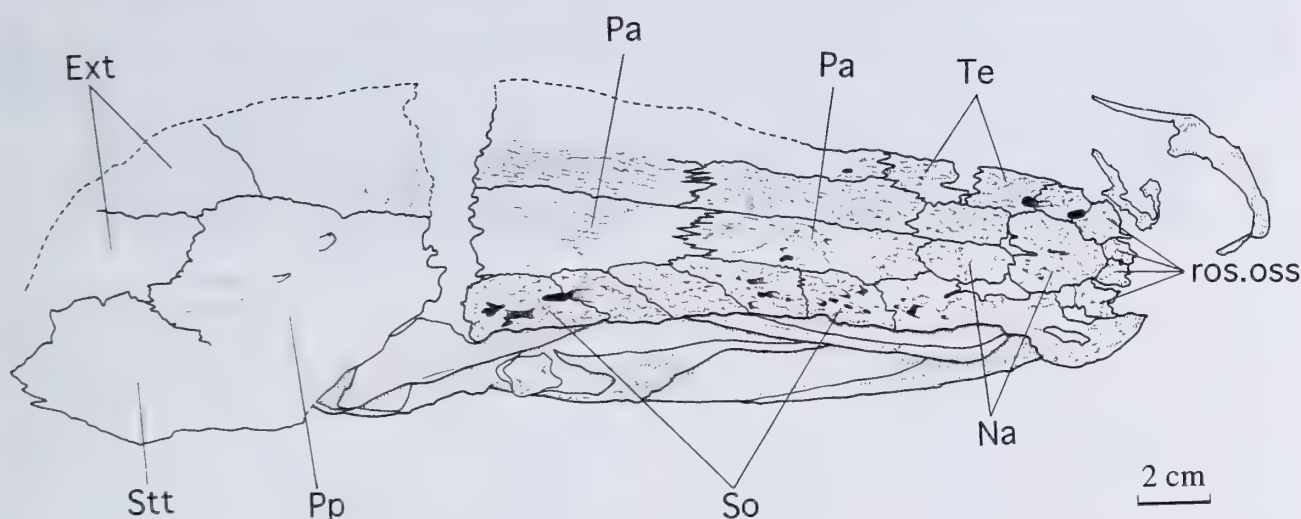
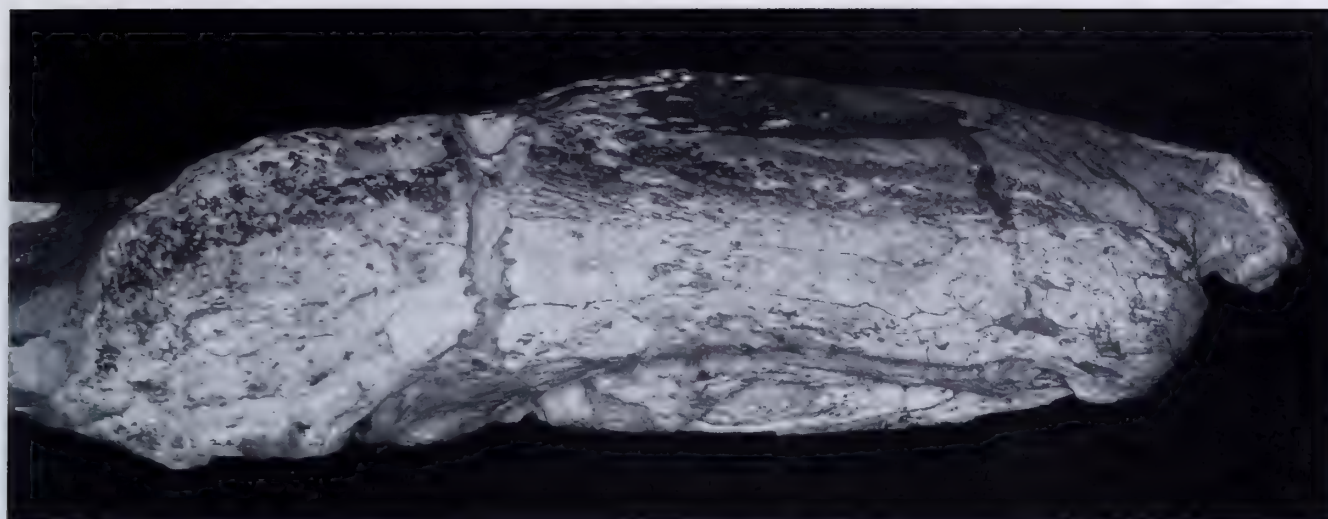
**Material.** — KMNH (Kitakyushu Museum of Natural History and Human History) VP 100,247, holotype, an almost complete, articulated specimen preserved in a calcareous concretion.

**Type locality.** — Exact locality not recorded, Araripe Plateau, Brazil. The type horizon is probably the Romualdo Member of the Santana Formation, which has yielded many fish fossils preserved in the same type of calcareous concretions as was the holotype. Although the age of this formation is considered to be Cretaceous, there are different opinions as to its exact age—Aptian (Santos and Valenca, 1968), Albian (Lima, 1979), Aptian-Albian (Schobbenhaus and Campos, 1986), older Neocomian (Maisey, 1986), Aptian-Albian (Maisey, 1991) and early Cenomanian (Martill, 1990).



Figure 1. *Mawsonia brasiliensis* sp. nov., holotype (KMNH VP 100.247, 1277 mm SL) from the Romualdo Member of the Santana Formation in the Araripe Plateau, Brazil.





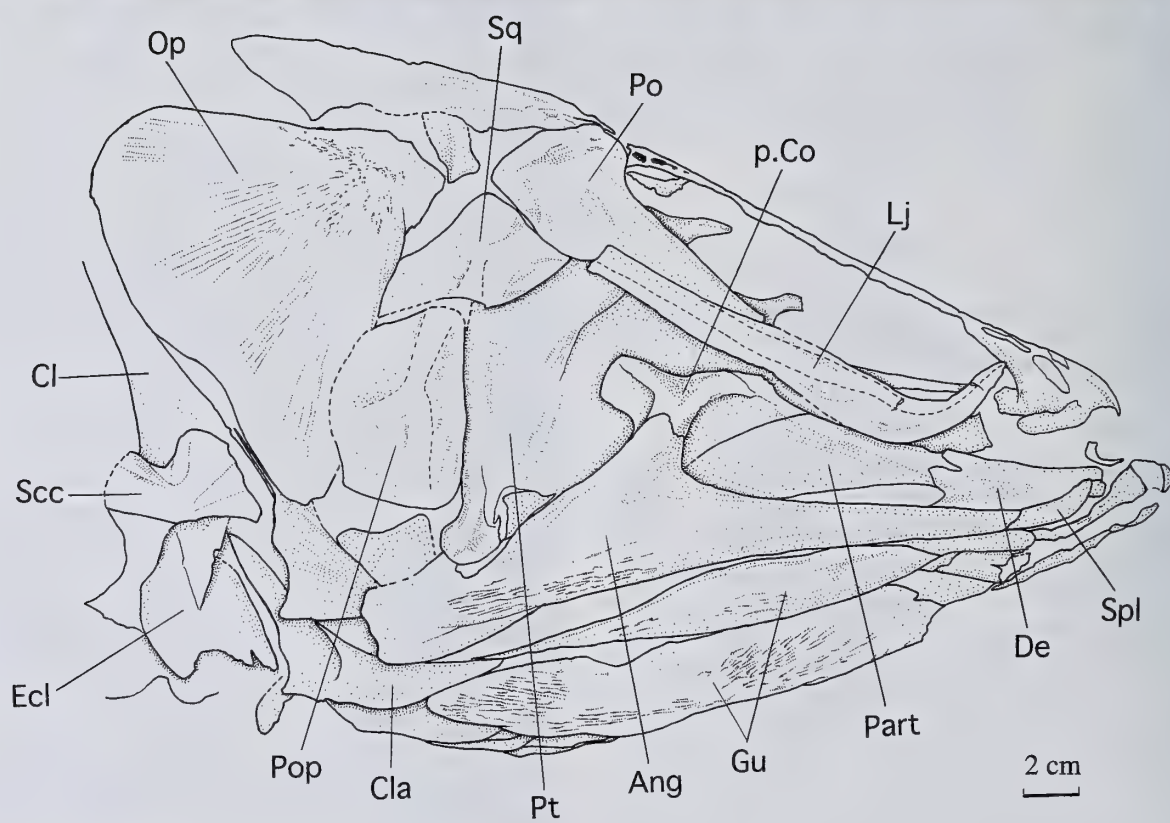
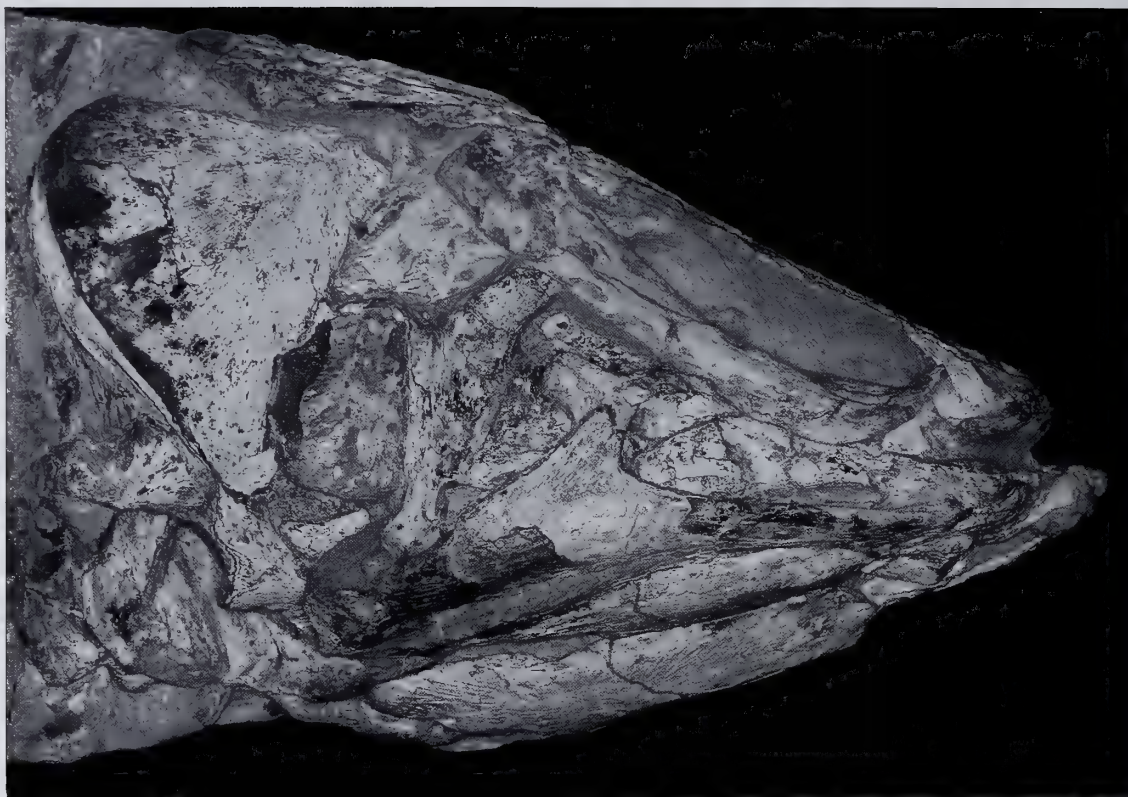
**Figure 2.** *Mawsonia brasiliensis* sp. nov., skull in dorsal view, holotype (KMNH VP 100,247, 1277 mm SL) from the Romualdo Member of the Santana Formation in the Araripe Plateau, Brazil. Abbreviations: Ext = extrascapular; Na = nasal; Pa = parietal; Pp = postparietal; ros.oss = rostral ossicles; So = supraorbital; Stt = supratemporal; Te = tectal.

**Etymology.**—The species is named for the country in which the specimen was found.

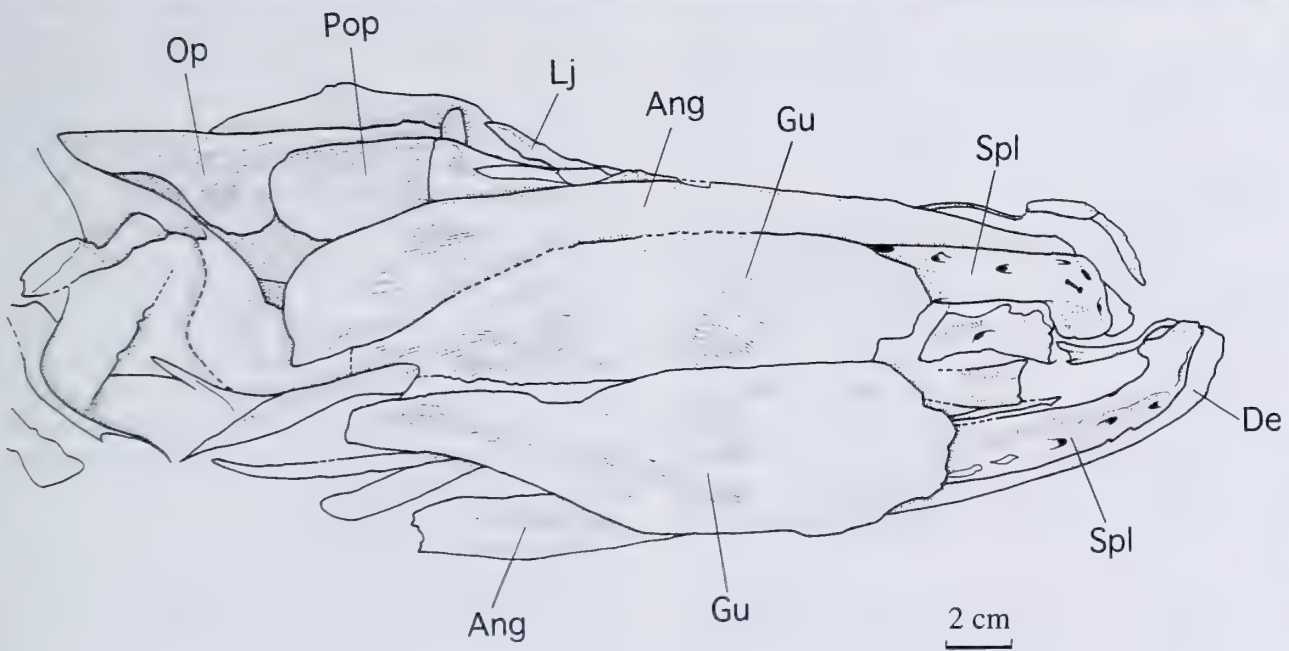
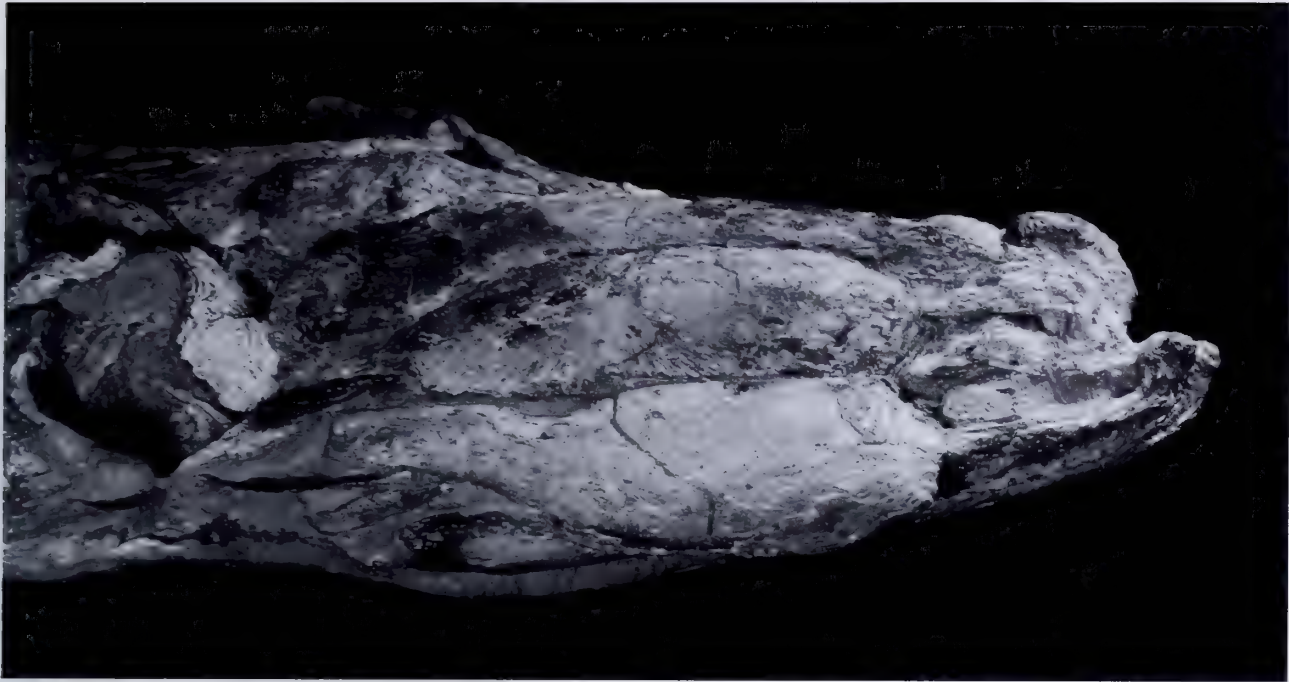
**Diagnosis.**—Length of the parietonasal shield is about twice its width. Its size is about 1.5 times that of the postparietal shield. Width of the postparietal shield is about 1.2 times its length. The fossa for the otic canal (foc) is present on the lateral surface of the postparietal and close to the small anterior apophysis (apa). The oval gular plate has no ridge running from the anterior to posterior ends. The ridges on the operculum are radial and weak. The angular is deep at its posterior, steep at the posterior dorsal edge, narrow at its anterior, and its anterior dorsal margin (where it articulates with the principal coronoid and

prearticular) is deeply concave. The scales are thin and have fine bony ridges (circuli) on the exposed portion, but have no ornamental tubercles or ridges typical of coelacanths.

**Description of holotype.**—The body is slender; body depth at the origin of the first dorsal about 300 mm; total length 1435 mm; standard length 1277 mm; head length 375 mm. Length of the parietonasal shield is 185.6 mm, the posterior end being broader, width of the right half 43.1 mm. Both parietals are narrow, the posterior one is wider, but the anterior one is just a bit longer. There is one anterior nasal, possibly fused, which is almost the same width as the width of the posterior nasals. The paired posterior







**Figure 4.** *Mawsonia brasiliensis* sp. nov., skull in ventral view, holotype (KMNH VP 100,247) from the Romualdo Member of the Santana Formation in the Araripe Plateau, Brazil. Abbreviations: Ang = angular; De = dentary; Gu = gular plate; Lj = lachrymojugal; Op = operculum; Pop = preoperculum; Spl = splenial.

← **Figure 3.** *Mawsonia brasiliensis* sp. nov., skull in lateral view, holotype (KMNH VP 100,247) from the Romualdo Member of the Santana Formation in the Araripe Plateau, Brazil. Abbreviations: Ang = angular; Cl = cleithrum; Cla = clavicle; De = dentary; Ecl = extracleithrum; Gu = gular plate; Lj = lachrymojugal; Op = operculum; Part = prearticular; p.Co = principal coronoid; Po = postorbital; Pop = preoperculum; Pt = pterygoid; Scc = scapulocoracoid; Spl = splenial; Sq = squamosal.

nasals are short, about 40% the length of the anterior parietals, and about 2.5 times their own width.

The paired posterior and anterior tectals are separated by a small space and are almost the same size, 22.5 mm in length and 16 mm in width. While the left tectals are well preserved, the right pair are slightly broken. The anterior tectal suture has posterior and anterior nasals and posterior rostral ossicles, while the posterior tectal suture has anterior parietals and posterior nasals. Each anterior tectal has a foramen which opens forward.

There are three pairs of rostral ossicles, all attached to the anterior nostril. While the anterior ossicles are small, 10.1 mm in length, 5.9 mm in width, the posterior and middle rostral ossicles are almost the same size: posterior pair 17.8 mm in length, 12.5 mm in width; middle pair 18.2 mm in length, 14.5 mm in width. There is a relatively large foramen, 5.2 mm long, between the posterior and middle rostral ossicles. The middle rostral ossicles also possess a foramen. There is a groove between the middle and anterior rostral ossicles.

Four supraorbitals are present, all about the same width. While the outline of the left supraorbitals is not distinct because the surface is broken, the right ones are well preserved. The length of the most anterior supraorbital is longest, 67.0 mm, about 1.5 times that of the others. Each supraorbital possesses a small foramen. Most of the first supraorbital attaches to the anterior parietal, but the posterior end attaches to the posterior parietal. The other supraorbitals attach to the posterior parietal.

The postparietal shield consists of a pair of postparietals, supratemporals and extrascapulars, the middle extrascapular being absent. Although most of the postparietals are broken, the suture between each bone can be recognized, except for the portion between the postparietal and supratemporal. About half of the left side and half of the right surface of the postparietal shield are missing. Of this shield, the postparietal, with two short processes on the anterior ventral surface, is the largest bone with a length of 76.7 mm. The width of the right extrascapular is 30.1 mm.

All cheekbones are well preserved. The postorbital, with a length of 119.2 mm and a height of 54.1 mm, has a long anterior process ventrally, extending 71.7 mm to the middle of the lachrymojugal. The depth at the base of the process is 21.1 mm. While the upper edge of the squamosal at 36.7 mm width is almost twice that of the lower edge, the depth is 53.8 mm. The preoperculum is deep, with a depth of 62.2 mm, about 1.5 times the width (44.5 mm). It is also narrow and round at the upper margin and along the lower margin of the squamosal. A sensory canal forks into two at the center of the preoperculum. The lachrymojugal is 149.1 mm long. Its anterior end curves upward, and a sensory canal runs along the upper

margin of this curved part.

The mentomeckelian is short, 42.2 mm in length, thick (13.7 mm) at the anterior end, and thin (2.8 mm) at its posterior.

The dentary lies outside the mentomeckelian and the lateral swelling is absent. It is long (left dentary 140.6 mm), almost half that of the mandible, curves medially at the anterior part, and the surface overlapping the angular is long. The upper limb of the dentary (81.7 mm in length) is short and contacts the prearticular, while the lower limb is long and occupies almost half of the mandible. There are two tooth plates on the dentary, but even though all the teeth are missing, many alveoli are visible, a few are 1 mm deep, and the rest of them minute.

The angular is long (from the anterior end of the inside to the posterior end of the outside, 149.2 mm), its deepest part is slightly behind the middle of the mandible, and at this point, the suture has a principal coronoid, forming a dorso-anterior process. Anterior to this point, it abruptly narrows, while posteriorly it gradually narrows, its depth posteriorly being almost twice that at the anterior.

The 72.2 mm long principal coronoid consists of anterior and posterior portions separated by a narrow section (24.3 mm deep) at the middle where the suture has the angular. The anterior portion has an almost triangular shape, and its antero-ventral margin contacts the prearticular. The posterior portion is rectangular with a depth of 16.9 mm and a length of 26.0 mm from the narrow section. The dorsal part of the posterior portion also forms a ridge that continues to the angular.

The anterior portion of the prearticular joins with the dentary and angular on the distal surface of the jaw to form a large foramen, while its posterior portion contacts the angular ventrally and the principal coronoid dorsally. Its deepest part, at 26.2 mm, is just behind the lateral midpoint.

The articular is small, 16.8 mm in depth, 24.4 mm long, and separated from the retroarticular. It joins with the retroarticular ossification to form glenoid articulation with a quadrate.

The right splenial is well preserved, its length about 5 times the width, and has five sensory canal openings. It contacts the ventro-mesial face of the dentary, and its anterior end curves mesially. While the width of the anterior end is 20.6 mm and the length 93.6 mm, the posterior portion gradually broadens to 18.8 mm.

The pterygoid, quadrate, and metapterygoid (including the anterior portion of the articular surface for the antotic surface) are exposed, but the pterygoid is covered for the most part by the lachrymojugal and lower jaw. Also, the border between the pterygoid and metapterygoid is covered by the postorbital and lachrymojugal. The quadrate has a slightly twisted upper portion, and articulates with the lower jaw by condyles the distal one of which is exposed.



There is a short dorso-anterior process on the upper end of the metapterygoid.

The cleithrum, extracleithrum and clavicle are well preserved. While the cleithrum is long and reaches up to about the level of the upper edges of the operculum, its upper portion has a cylindrical shape while its lower portion is broad and complicated in structure. Also a flange extends outward and backward at the antero-ventral portion of the cleithrum. Its triangular postero-ventral portion joins with the extracleithrum to form a postero-ventral section of the shoulder girdle. The extracleithrum is a broad bony plate and slightly curves anteriorly. The clavicle contacts the ventral edge of the cleithrum and the anterior edge of the extracleithrum. It consists of anterior and posterior flanges, the latter being narrow along the dorsal edge. The anocleithrum is not preserved in this specimen.

The scapulocoracoid, shaped like a twisted bowtie, is preserved on the cleithrum slightly below the middle of the cleithrum, and is slightly apart from extracleithrum.

The triangular operculum extends slightly antero-ventrally, while its postero-ventral margin becomes slightly concave below the middle of the margin. Its anterior margin is thick, being thickest at the dorsal end. Most of the opercular surface is missing, but weak radiating ridges are visible.

The first dorsal fin with 10 fin rays is well preserved. Its basal plate, 92.5 mm long and 40.8 mm deep, is kidney-shaped with the anterior portion slightly extended, deepest at slightly behind the midpoint, while the posterior dorsal edge supports the dorsal fin rays. The depth of the anterior end of the plate is 16.7 mm. The first five fin rays articulate with the thick edge which fans out from the portion slightly behind the center of the plate. From this portion a weak ridge runs forward.

The second dorsal fin rays are not preserved. Its basal plate has two anterior branches, the upper branch at 72.5 mm being longer and more slender than the lower (54.0 mm). The length of the preserved part is 112.9 mm. Even with the very end missing, it can be seen that the posterior portion of the basal plate is broad.

Both pectoral fins are preserved. The right pectoral fin with thirty-two countable fin rays is preserved behind the head and covers the anterior part of the basal plate of the dorsal fin. Twenty-five rays can be counted on the portion of the left pectoral fin preserved below the right pelvic girdle.

Three bones of the pelvic girdle are preserved above the middle of the left pectoral, the most anterior one being the largest and T-shaped, and consisting of three processes. The posterior end of the bone is missing. Its anterior process abruptly becomes narrow anteriorly, while the dorsal process is shorter than the ventral process, and slightly curves backward. Two small bones behind the large pel-

vic bone are considered to be axial mesomeres of the pelvic girdle. The anterior portions of the mesomeres are missing; however what remains of the ventral cylindrical one gradually thickens posteriorly. It is larger than the dorsal one. Twenty-two fin rays can be counted in the left pelvic fin. A part of the right pelvic fin is preserved on the ribs. The first anal fin is missing.

The centra are unossified. Their anterior neural spines are short and pebble-like, but the posterior ones are longer. Neural spines that articulate with pterygiophores of the third dorsal fin are long and stout at the dorsal end. The base of the neural spines is divided and forms the neural arches. There are 20 neural spines for the third dorsal pterygiophores and 33 anterior to them. Twenty-three relatively long, slender ribs are found along the dorsal margin of the swim bladder.

There are 23 third dorsal fin rays. Four haemal spines can be identified anterior to the first pterygiophore of the second anal fin. Fifteen haemal spines reach to the 21 pterygiophores of the second anal fin. The number of second anal fin rays is 25.

Only part of the caudal fin is preserved. The posterior end is missing. Four rays of the upper lobe and 7 rays of the lower lobe are preserved.

Scales are thin and well preserved, but no typical coelacanth tubercle or ridge ornamentation is visible, except for fine bony ridges (circuli) on the exposed portion.

*Remarks.*—Cloutier and Forey (1991) recognized the following five species in the genus *Mawsonia*: *M. gigas* Woodward, 1907, *M. tegamensis* Wenz, 1975, *M. ubangiana* Casier, 1961, *M. lavocati* Tabaste, 1963, and *M. libyca* Weiler, 1935. *M. gigas* was described from South America, the others from Africa. Maissey (1986) described the specimen AMNH 11758, acid-prepared bones: parietonasal and postparietal shields, right postorbital, squamosal, lachrymojugal, incomplete operculum, pterygoid, metapterygoid, quadrate, autopalatine, and coronoid from a single specimen as *M. cf. gigas*. The author compared the present specimen with specimen AMNH 11758 and now regards it as *M. brasiliensis*, because the proportions of these bones are the same. The specimen AMNH 11758 has the fossa for the otic canal of the postparietal on the lateral surface of the postparietal close to the anterior apophysis.

On the basis of the following characters, this new species belongs to the genus *Mawsonia*: length of the parietonasal shield is about 1.5 times the length of the postparietal shield, postorbital (dermosphenotic in Maissey, 1986) has a splint-like anterior projection, posterior two-thirds of the elongated lachrymojugal is almost straight.

This new species differs from *M. tegamensis* from the Aptian of Niger in having the length of the parietonasal shield twice (versus 1.7 times) its width and 1.5 times (ver-



sus 1.4 times) the length of the postparietal shield; width of the postparietal shield 1.2 times (versus 1.6 times) its length; long, oval gular plates versus gular plates with a wide, rather than slender, anterior portion; radial ornamentation on the anterior portion of the operculum versus a mesh-like pattern.

This new species differs from *M. ubangiana* from the Neocomian of Zaire in having the fossa for the otic canal of the postparietal (parietal in Maisey, 1986) on the lateral surface of the postparietal close to the anterior apophysis. In *M. ubangiana*, the fossa is present on the ventral surface of the postparietal distant from the anterior apophysis of the postparietal.

In *M. lavocati* from the Albian of Morocco, the anterior end of the angular is higher than that of the new species, and the angle between the postero-dorsal edge and the ventral edge of the angular is larger. Also, the ornamentation in *M. lavocati* is more pronounced.

This new species differs from *M. libyca* from the Albian of Egypt in having the dorsal edge of the angular deeply concave at the midpoint versus slightly concave.

Although this new species is close to *M. gigas* from the Neocomian of Bahia, Brazil in appearance, it differs in having the small anterior apophysis of the postparietal and the fossa for the otic canal close to the anterior apophysis versus a large anterior apophysis of the postparietal and the fossa for the otic canal distant from the anterior apophysis of the postparietal; the antero-lateral surface of the postparietal forming a steep (versus gentle) slope; the angular being deeper; and no ridge running from the anterior to posterior ends on the gular plates.

This new addition to the genus *Mawsonia* is significant in increasing understanding of the diversity of the suborder Latimerioidei in the early Cretaceous, which lineage continues to the Recent coelacanths of the genus *Latimeria*.

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# *Echigoceras sasakii*, a new Middle Carboniferous nautilid from the Omi Limestone Group, Central Japan

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**Abstract.** A new genus and species of the trigonoceratid nautilid, *Echigoceras sasakii*, is described. Specimens of this cephalopod occur in the Middle Carboniferous (probable late Bashkirian) bioclastic rudstone/grainstone of the Omi Limestone Group, Central Japan. *Echigoceras* is most closely related to the Early Carboniferous genus *Stroboceras*, but differs in its strongly curved cyrtconic shell and siphuncular position near the ventral margin. It is possible that *Echigoceras* is the descendant of *Stroboceras*.

**Key words:** *Echigoceras* gen. nov., Middle Carboniferous, Nautiloidea, Omi Limestone Group, Trigonoceratidae

## Introduction

Following Niko (2001), the present report on a new trigonoceratid nautilid genus and species is the second installment in a series describing the Carboniferous cephalopod fauna of the Omi Limestone Group in Niigata Prefecture, Central Japan. All of the material documented herein is from the light gray, massive limestone belonging to bioclastic rudstone/grainstone of Middle Carboniferous (probable late Bashkirian) age at the southern corner of Higashiyama Quarry, the identical locality to that for the previously described orthoconic forms (Niko, 2001). The material is deposited in the University Museum of the University of Tokyo (UMUT).

## Systematic paleontology

Order Nautilida Agassiz, 1847

Superfamily Trigonoceratoidea Hyatt, 1884

Family Trigonoceratidae Hyatt, 1884

Genus *Echigoceras* gen. nov.

*Type species.*—*Echigoceras sasakii* sp. nov., by monotypy.

*Diagnosis.*—Trigonoceratid with strongly curved cyrtconic shell whose surface is indented by longitudinal ridges and grooves; gross profiles of whorl are mostly subtrapezoidal, with inflated dorsal side; lobed peristome preserved as distinct growth lines characterized by V-shaped ventral sinus; siphuncular position near ventral margin;

septal necks orthochoanitic, with very narrow septal foramina.

*Etymology.*—The generic name is derived from Echigo, which is a historic provincial name for the type locality.

*Echigoceras sasakii* sp. nov.

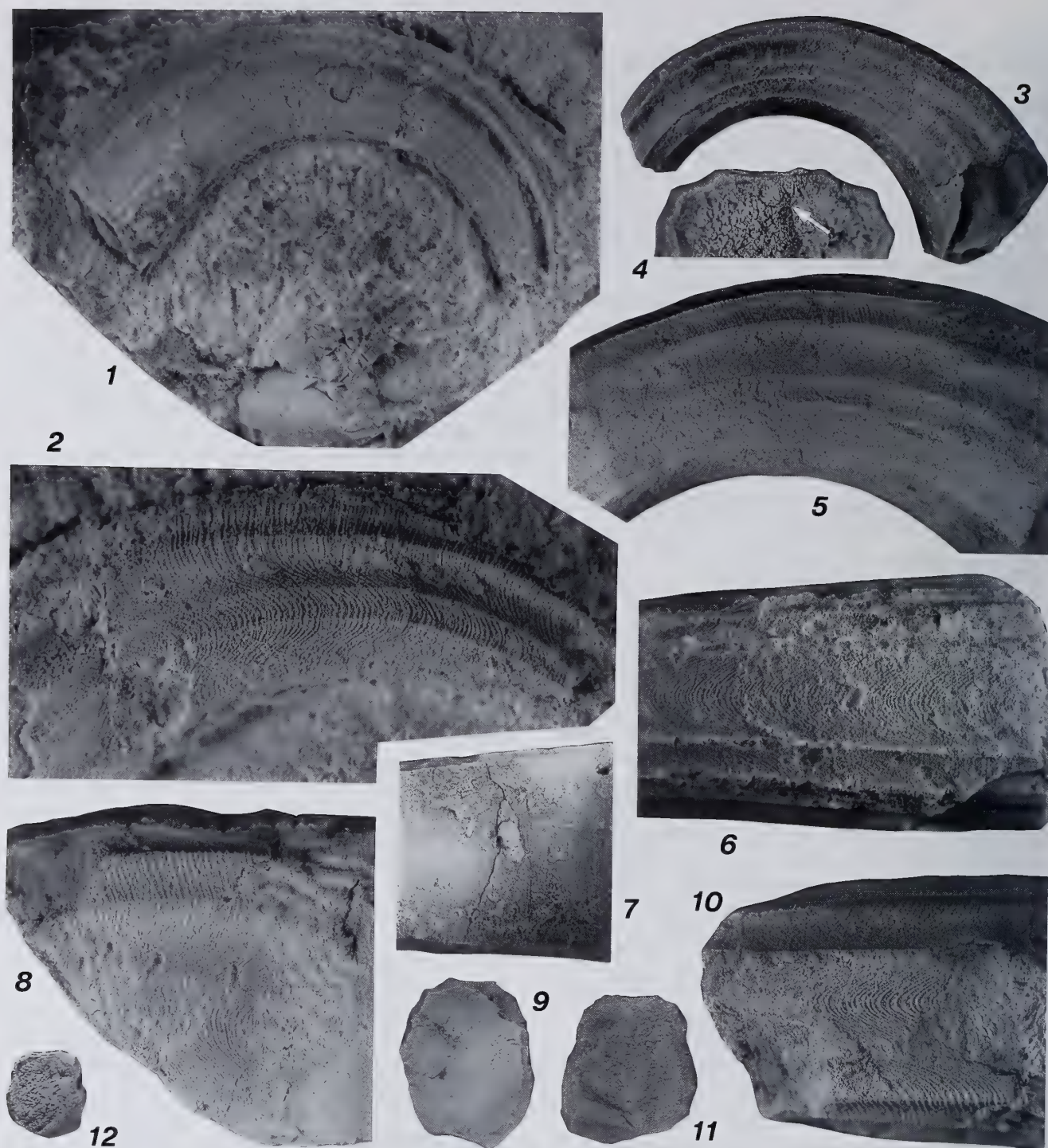
Figures 1–4

*Stroboceras* sp., Oyagi, 2000, p. 108.

*Diagnosis.*—Same as for the genus.

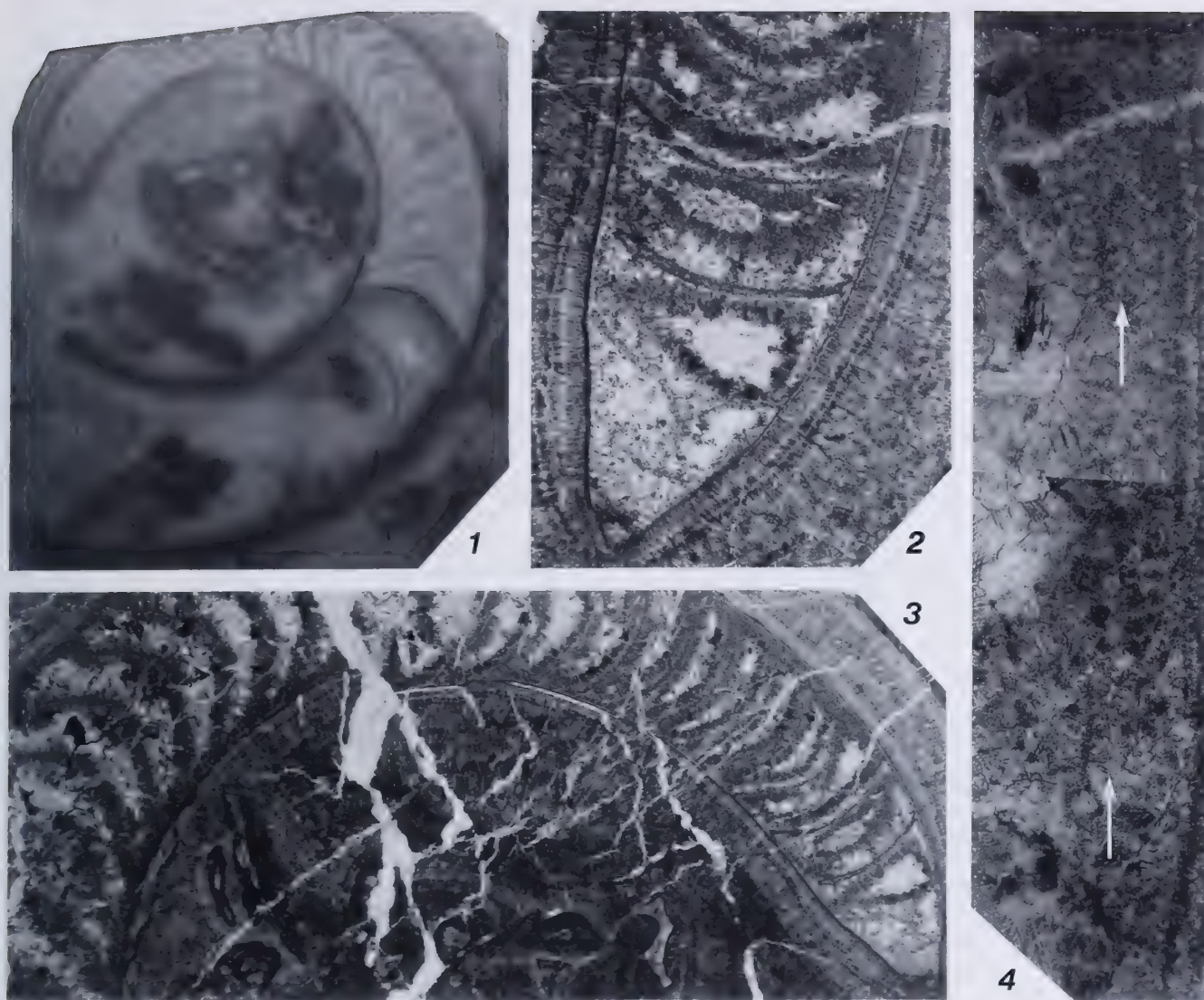
*Description.*—Strongly curved, horseshoe-like cyrtcones consisting of less than one full circle, comprising approximately 0.91 of a full circle; shell size moderate for the family, maximum whorl diameter of holotype 45.0 mm; gross profiles of whorl are mostly subtrapezoidal with broadly inflated dorsal side and width/height ratio (form ratio) of approximately 0.94, then changing to laterally compressed suboval cross section near aperture, where whorl dimensions of 11.7 mm in width and 15.0+ mm in height give a form ratio of 0.78–; body chamber represented adorally by approximately one-third of whorl. Shell surface is indented by strongly prominent bilaterally symmetrical longitudinal ridges, as follows: 1 ventral (vr), 2 ventrolateral (v-lr1, v-lr2), 2 lateral (lr1, lr2), and 1 dorsolateral (d-lr); except for dorsal side of the shell, interspaces between longitudinal ridges are depressed and form longitudinal grooves; among these, there is a groove sandwiched between the ventrolateral and lateral longitudinal ridges (= between v-lr2 and lr1) that is deeply concave.





**Figure 1.** *Echigoceras sasakii* gen. et sp. nov. **1, 2.** Holotype, UMUT PM 27920; **1**, lateral view, aperture on left, apical shell embedded in matrix, and apertural shell partly removed,  $\times 2$ ; **2**, details of surface ornamentation,  $\times 4$ . **3–7, 11, 12.** Paratype, UMUT PM 27919; **3**, lateral view, aperture on right,  $\times 2$ ; **4**, enlargement of ventral margin of Figure 1.12, showing siphuncular position (arrow),  $\times 6$ ; **5**, details of surface ornamentation,  $\times 4$ ; **6**, ventral view showing details of surface ornamentation, aperture on right,  $\times 4$ ; **7**, dorsal view showing details of surface ornamentation, aperture on right,  $\times 4$ ; **11**, cross-sectional view of adoral end, venter up,  $\times 2$ ; **12**, cross-sectional view of apical end, venter up,  $\times 2$ . **8–10.** Paratype, UMUT PM 27921; **8**, lateral view, aperture on right, showing details of surface ornamentation and partial peristome,  $\times 4$ ; **9**, apertural view, venter up, dorsal shell partly lacking,  $\times 2$ ; **10**, ventral view, aperture on right, showing details of surface ornamentation,  $\times 4$ .



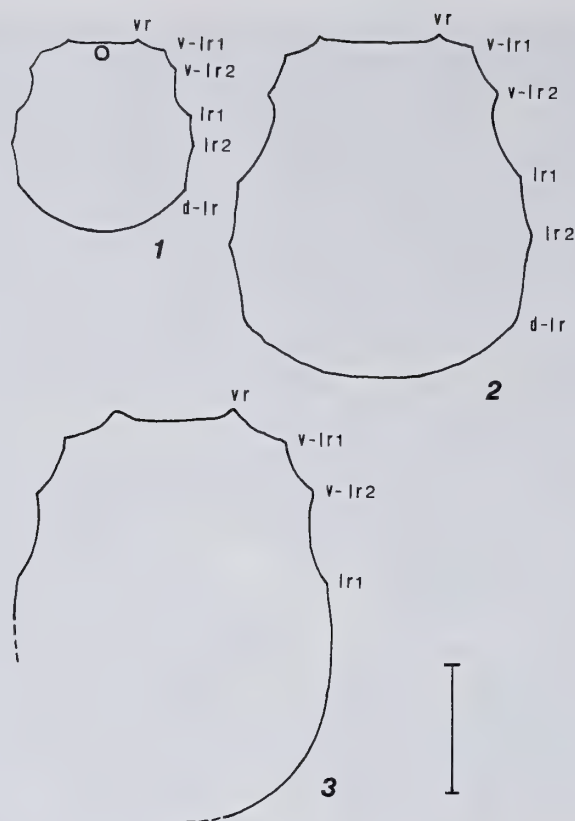


**Figure 2.** *Echigoceras sasakii* gen. et sp. nov. 1–4. Holotype, UMUT PM 27920, longitudinal sections; 1, polished section,  $\times 2$ ; 2, thin section showing embryonic shell, not through siphuncle,  $\times 10$ ; 3, thin section of apical shell,  $\times 5$ ; 4, thin section with arrows indicate the septal foramina,  $\times 25$ .

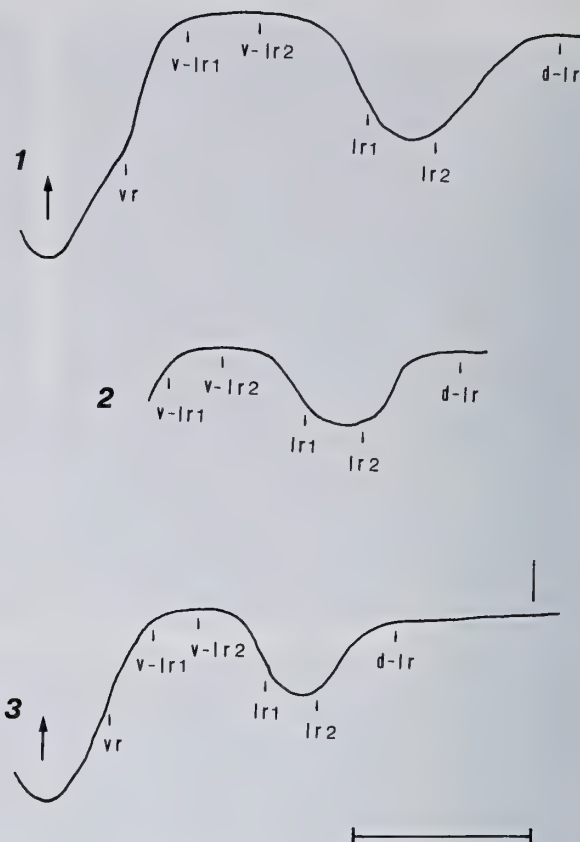
Peristome lobed, with deep, V-shaped ventral (hyponomic) sinus, broadly rounded ventrolateral saddle, moderately deep lateral (ocular) sinus and nearly transverse dorsal apertural rim; peristome preserved as distinct growth lines throughout shell; lateral and dorsolateral longitudinal ridges become subdued, and grooves between these ridges disappear near aperture. Judging from longitudinal section, embryonic shell probably is cone-shaped. Sutures not observable in all examined specimens, but serial longitudinal sections do not indicate distinguished obliquity and sutural elements. Cameral length moderate for family; there are 3 to 4 camerae in corresponding whorl height.

Septa moderately concave for family, and form retrochoanitic siphuncle near ventral margin; ratio of minimum distance of central axis of septal foramen from whorl surface per corresponding whorl height (siphuncular position ratio) is approximately 0.08; septal necks orthochoanitic and relatively short with 0.71 mm in well-preserved dorsal septal neck at whorl height of approximately 9.5 mm, where diameters of septal foramina are very narrow for family at approximately 0.32 mm; connecting rings probably tube-like. Cameral and endosiphuncular deposits absent.

*Discussion.*—An Early Carboniferous genus *Stroboceras*



**Figure 3.** *Echigoceras sasakii* gen. et sp. nov., diagrams from cross sections of whorls, venter up. 1, 2. Paratype, UMUT PM 27919; 1, phragmocone, note siphuncular position; 2, body chamber. 3. Paratype, UMUT PM 27921, body chamber near aperture. Abbreviations: vr = ventral ridge; v-lr1, v-lr2 = ventrolateral ridges; lr1, lr2 = lateral ridges; d-lr = dorsolateral ridge. Scale bar equals 5 mm.



**Figure 4.** *Echigoceras sasakii* gen. et sp. nov., diagrams of growth lines to show peristome shapes in relation to the positions of the longitudinal ridges. 1. Paratype, UMUT PM 27921. 2. Holotype, UMUT PM 27920. 3. Paratype, UMUT PM 27919. Positions of longitudinal ridges are indicated by symbols (see explanation of Figure 3). Scale bar equals 5 mm.

(Hyatt, 1884; type species, *Gyroceras harttii* [sic] Dawson, 1868) has the longitudinal ridges of, and a peristome outline similar to, *Echigoceras sasakii* gen. et sp. nov., and moreover all the outer whorls of *Stroboceras* are partly divergent each from the preceding one. Therefore, from fragmentary shells such as the present two paratypes (UMUT PM 27919, 27921), a distinction between *Echigoceras* and *Stroboceras* would be difficult to make based only on external morphology. In this case, the siphuncular position is the most diagnostic feature separating these genera; i.e., the position of the siphuncle near the ventral margin of the new genus contrasts with the siphuncular position of *Stroboceras*, which is subcentral to nearly midway between the center and the ventral margin. All trigonoceratids have cyrtconic stages in their early ontogeny. In particular, the early juvenile shell of *Stroboceras hartii* illustrated by Bell (1929) most closely resembles that of *Echigoceras sasakii*, and the cyrtconic

parts of *Catastroceras* (Turner, 1965; type species, *Nautilus quadratus* Fleming, 1828) and *Pseudocatastroceras* (Turner, 1965; type species, *Coelonautilus trapezoidalis* Jackson, 1919) also possess longitudinal ridges, but they are less than 20 mm in shell diameter.

Among the known nautilids *Echigoceras* has the most similar shell morphology to *Stroboceras* as alluded to in the above comparisons. In addition, the range of *Stroboceras*, Viséan to early Namurian of the Early Carboniferous (e.g., Gordon, 1964), was replaced by that of *Echigoceras*, for which a Middle Carboniferous (probable late Bashkirian) age is suggested. *Echigoceras* is the probable descendant of *Stroboceras*.

A figured specimen from the Omi Limestone Group cited as *Stroboceras* sp. by Oyagi (2000) is probably conspecific with *Echigoceras sasakii*. In addition, it should seem that *Stroboceras* sp. listed by Nishida and Kyuma (1986) from the Bashkirian to Moscovian of the



Akiyoshi Limestone Group, Southwest Japan, needs re-evaluation based on present knowledge. However, the specimens from these two localities are not presently available for re-examination.

*Etymology.*—The specific name honors the late Dr. Madoka Sasaki, in recognition of his contributions to the taxonomic study of living cephalopods.

*Material examined.*—The holotype, UMUT PM 27920, is a complete specimen. Unfortunately, attempts to separate the embryonic shell and apertural rim of the holotype from the well-indurated matrix were not successful. The following two paratypes of the fragmentary shells are assigned to the species: UMUT PM 27919, incomplete phragmocone with apical body chamber, 35.3 mm in length, and UMUT PM 27921, adoral body chamber including apertural rim, 15.9 mm in length.

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# Turrilitid ammonoid *Carthaginites* from Hokkaido (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin—XCIV)

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**Abstract.** This paper gives a revised definition of the genus *Carthaginites* Pervinquier, 1907 on the basis of material from Hokkaido, Japan, that enhances previously available material. Two species from the middle Cenomanian rocks of Hokkaido are described: *C. asiaticum* (Matsumoto and Takahashi, 2000) and *C. yamashitai* sp. nov. Brief comments are also made on some species which were previously described from the upper Cenomanian rocks of North America and Europe. Morphologically and stratigraphically *Carthaginites* is intimately related to *Neostlingoceras* Klinger and Kennedy, 1978, of early Cenomanian age.

**Key words:** *Carthaginites*, Cenomanian, Cretaceous, Hokkaido, *Neostlingoceras*, *Raynaudia*

## Introduction

A well preserved specimen of a turreted ammonite was collected by Minoru Yamashita and was provided to me for study in 1981, but it was left undescribed, because I failed to understand adequately its peculiar characters. Meanwhile my work on the turrilitid ammonoids proceeded step by step, mostly with coworkers, and in this connection I noticed that the species described as *Neostlingoceras asiaticum* Matsumoto and Takahashi, 2000 is peculiar in its very small size and much weaker ornamentation. I also noticed that its suture is so peculiar that my previous drawing should be revised. Thus, the genus *Carthaginites* Pervinquier, 1907 came to my mind. At the same time I became aware that the specimen provided by Yamashita is an excellent example of *Carthaginites*. These two species came from the middle, instead of the lower, part of the Cenomanian. In this paper the results of my study are presented in the customary style of systematic description.

**Conventions.**—The specimens from Hokkaido described in this paper are kept at the Kyushu University Museum under the heading GK. Other specimens mentioned are cited according to the usual form used for the given institutions.

Sutural elements are designated E, L, U, and I for the external, lateral, umbilical and internal lobes, following normal usage for the group.

## Systematic descriptions

Order Ammonoidea Zittel, 1884  
Suborder Ancyloceratina Wiedmann, 1966  
Superfamily Turrilitoidea Gill, 1871  
Family Turrilitidae Gill, 1871  
Genus *Carthaginites* Pervinquier, 1907

**Type species.**—*Turrilites* (*Carthaginites*) *kerimensis* Pervinquier, 1907 (p. 101, pl. 4, figs. 18, 19; text fig. 29) by original designation (Pervinquier, 1907, p. 96).

**Diagnosis.**—Small turreted shell, with low apical angle; surface in early growth stage nearly smooth, with a shallow median spiral depression; later row of faint nodes discernible above the median depression and another row of numerous, tiny tubercles along the lower whorl seam. Suture abnormal in showing L and in part E/L and L/U saddles on the exposed whorl face, without full half of E. In other words, the siphuncle does not run along the upper edge of the whorl but deviates at some distance toward the umbilical margin of the preceding whorl.

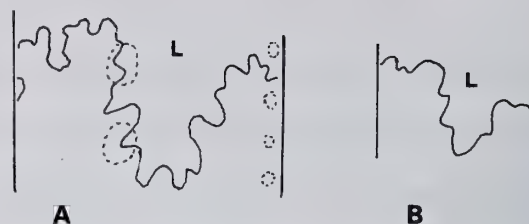
**Discussion.**—*Carthaginites* was proposed by Pervinquier (1907, p. 96) as a subgenus of *Turrilites* Lamarck, 1801. It was raised to the rank of a full genus by Dubourdieu (1953, p. 44), who erected another species *Carthaginites krorzaensis* Dubourdieu (1953, p. 66, pl. 4, figs. 49–52, text-fig. 20) on the basis of a single isolated whorl, which is about 3 mm in height and 5 mm in diameter. There is a very shallow spiral depression at midflank

and a row of narrow clavi along the lower whorl seam. Owing to the isolated condition of the whorl, the suture was fully illustrated from the umbilicus of the lower surface, via the whorl flank, to the upper surface, and the position of the siphuncle is shown much apart from the angle of the upper whorl seam to the vicinity of the umbilicus of the upper surface (see Dubourdieu, 1953, text-fig. 20).

The features described above are the most important characters of the genus *Carthaginites*. It should be also noted that the suture is not necessarily simple but moderately incised like that of immature *Ostlingoceras* (see fig. 2 in Matsumoto and Takahashi, 2000). Generally the degree of sutural incision depends on species, growth stage and mode of preservation or effect of weathering. In any event, in regard to the above points Wright and Kennedy (1996, p. 361) seem to have inadequately presented the generic diagnosis. However, I agree with them in their allotment of their British specimen (BMNH C76469) (Wright and Kennedy, 1996, p. 361, pl. 98, fig. 11) to the genus *Carthaginites*.

Dubourdieu (1953, p. 67) and also Wright and (Kennedy 1996, p. 361) described the distinction between *Carthaginites* and *Raynaudia* Dubourdieu, 1953 (type species *Turrilites* (*Carthaginites*) *raynaudiensis* Collignon (1932, p. 19, pl. 1, figs. 22–25; text-figs. 24–26). Dubourdieu (1953, fig. 13) presumed that *Carthaginites* evolved from *Raynaudia*, but no substantial evidence was given. Judging from the shell form and ornamentation, *Carthaginites* is related more closely to *Neostlingoceras* Klinger and Kennedy, 1978 (type species *Turrilites* *carcitanensis* Matheron, 1842). Generally the former is smaller and more faintly ornamented than the latter. The unusual position of the siphuncle and the consequent abnormal disposition of the sutural elements are particular to *Carthaginites*.

**Distribution.**—The type species (*C. kerimensis*) was recorded by Pervinquier (1907, p. 101) from the “Vraconian” of Tunisia, but it is regarded as a late Cenomanian species by Wright and Kennedy (1996, p. 361). *C. krorzaensis* is from the upper Cenomanian rocks in the neighbourhood of Djebel Quenza, SE of Djebel Krorza in Algeria (Dubourdieu, 1953, p. 68). The British specimen (*vide supra*) is from the upper Cenomanian *Calycoceras guerangeri* Zone of Devon, southern England (Wright and Kennedy, 1996, p. 363). The two species from Hokkaido (northern Japan), described below, came from the middle Cenomanian *Calycoceras* (*Newboldiceras*) *asiaticum* Zone. Some of the species described under *Neostlingoceras* from the upper Cenomanian rocks of the North American Western Interior region are to be transferred to *Carthaginites* (see discussion below).



**Figure 1.** *Carthaginites asiaticus* (Matsumoto and Takahashi), Sutures on the whorl flank. A. GK H8536 (holotype),  $\times 10$ . B. GK. H8537 (younger paratype),  $\times 12$ .

### *Carthaginites asiaticus* (Matsumoto and Takahashi, 2000)

Figure 1

*Neostlingoceras asiaticum* Matsumoto and Takahashi, 2000, p. 266, figs. 5A–C, D–F, G; 6.

**Material.**—GK. H8536 (holotype), GK. H8537 and GK. 8538, collected by T. Takahashi (for more details see Matsumoto and Takahashi, 2000, p. 266).

**Revised diagnosis.**—Shell slender with a low apical angle; whorl at early growth stage rather smooth, with rounded upper shoulder, shallow spiral groove at midflank, and sharply demarcated lower edge. Later, a row of blunt nodes developed on the upper part, with shallow spiral groove below it, and numerous, minutely pointed clavate tubercles along the lower whorl seam. Sutural element L exposed at about the middle of the flank, whereas E and U are unexposed on the flank; siphuncle situated at some distance from the upper edge of the whorl flank, running below the unexposed roof of the whorl.

**Measurements.**—See Matsumoto and Takahashi 2000, table 3.

**Remarks.**—The suture of the newly prepared part of the holotype (GK. H8536) is shown in Figure 1A; that of the paratype (GK H8537) in Figure 1B. The latter was incorrectly drawn in Matsumoto and Takahashi (2000, fig. 6) on account of the incomplete cleaning of the shelly material in the zones along the upper and the lower seams of the whorl.

Based on the above revision, *Neostlingoceras asiaticum* Matsumoto and Takahashi should now be called *Carthaginites asiaticus* (Matsumoto and Takahashi).

**Discussion.**—As in the case of Hokkaido, some of the species described under *Neostlingoceras* from the upper Cenomanian rocks in the Western Interior of North America described by Cobban *et al.* (1989) should be reexamined. As I have had no opportunity to examine the original specimens, I merely give suggestions. *N. procerum* Cobban, Hook and Kennedy (1989, p. 60, figs 62, 95 O–Q, S) from the upper Cenomanian *Metoicoceras mosbyense* Zone is probably an example of *Carthaginites*,





Figure 2. *Carthaginites yamashitai* sp. nov. Lateral views (A–E anticlockwise turned) and basal view (F) of GK. H8539 (holotype),  $\times 3$ . Photos courtesy of T. Nishida.



Figure 3. *Carthaginites yamashitai* sp. nov. Sutures on the flank of three successive whorls of GK. H8539 (holotype),  $\times 8$ .

because it has a small and feebly ornamented shell and abnormal configuration of the suture. *N. bayardense* Cobban, Hook and Kennedy (1989, p. 60, figs. 95R, 96R) from the same zone may be another species of *Carthaginites*, although its suture was not illustrated.

**Occurrence.**—The holotype and the two paratypes of this species came from Loc. Ik 1103 (for the location see

Matsumoto and Takahashi, 2001, fig. 4), where the middle Cenomanian Zone of *Calycoceras* (*Newboldiceras*) *asiaticum* Zone is exposed.

#### *Carthaginites yamashitai* sp. nov.

Figures 2 and 3

**Material.**—Holotype is GK. H8539 (Figure 2) collected by Minoru Yamashita from a cutting, SE of Poronai, Mikasa district and later donated to the Kyushu University Museum. This is well preserved, but no other specimens are available.

**Diagnosis.**—Small flat-sided turricone, with estimated apical angle of  $18^\circ$ . Young whorls look almost smooth, but for faint spiral depression at midflank and numerous minute tubercles aligned immediately above the lower whorl seam. In later growth stages blunt major tubercles developed above the spiral depression and minor ones along the lower whorl seam. The latter are pointed at their top immediately above the lower whorl seam but

clavate at their base, forming a wavy spiral line. Thus, a kind of double feature is shown. Configuration of the sutural elements abnormal in showing the entire L and parts of the saddles E/L and L/U on the exposed whorl face; E almost entirely unexposed on the flank (Figure 3).

**Description.**—This single available specimen consists of 9 whorls, without the youngest part and the destroyed last portion of the body chamber. It is 27 mm in total height, and the diameter of the last whorl is 10 mm. Each whorl is trapezoidal in lateral view, with the larger dimension along the lower row of small tubercles. For instance, the ratio of height to lower diameter is 0.45 and of height to upper diameter 0.50.

The shallow spiral depression is better discernible on the internal mould. It is at about the midflank in young whorls and gradually shifted downward with growth. I notice a questionable feature that several minutely pointed upper tubercles are discernible in a part of the preserved first whorl (see Figure 2C, D). Whether this is a constant character or merely accidental cannot be decided without examining more specimens.

In later growth stages major tubercles of the upper row may be somewhat bullate upward. The tubercles of the lower row are small but fairly distinctly pointed and slightly bullate upward. They are twice as numerous as the nodes of the upper row; for instance 30 against 15 in the whorl of the middle growth stage. They rest on a wavy spiral ridge which forms an edge between the flank and the lower face of the whorl. On the basal face of the preserved last whorl a radial rib runs from each wave of the ridge toward the umbilicus with gentle curvature (Figure 2F).

The suture on the flank of the successive three whorls is illustrated in Figure 3.

**Comparison.**—This species is undoubtedly referred to *Carthaginites* on account of its small size, faint ornamentation with a shallow spiral groove at about the midflank and the deviation of the siphuncle from the upper edge of the whorl flank inward below the upper whorl face as shown by the particular configuration of the sutural elements.

The estimated apical angle of *C. yamashitai* is larger than that in *C. kerimensis* and *C. asiaticus*. As to the degree of minor sutural incisions, there is no significant difference between *C. yamashitai* and *C. krorzaensis* or *C. asiaticus*, if the gradual change with growth is taken into consideration. The gradual change of ornamentation with growth in this species is analogous to that of *C. asiaticus*. The two species are distinguished by the difference in the whorl shape and the style of ornamentation.

**Occurrence.**—The holotype was collected from the middle Cenomanian *Calycoceras* (*Newboldiceras*) *asiaticum* Zone exposed at a cutting of a forestry road, about 3500 m S60° E from the Poronai colliery, Mikasa district. This

fossil locality is marked in the official geological map "Iwamizawa" (Matsuno *et al.*, 1964). I went there later but failed to obtain additional material. The fossiliferous bed is referred to the Mikasa Formation which consists mainly of sandy sediments of shallow sea facies.

### Concluding remarks

(1) The genus *Carthaginites* Pervinquier, 1907 was previously represented by small and more or less incompletely preserved specimens of rare occurrence from Tunisia and Algeria. In addition to the original works of Pervinquier (1907) and Dubourdieu (1953) the better preserved specimens from Hokkaido are taken into consideration, and thus the diagnosis of the genus *Carthaginites* is given clearly in this paper.

(2) The species previously called *Neostlingoceras asiaticum* Matsumoto and Takahashi, 2000 is revised in this paper to *Carthaginites asiaticus* (Matsumoto and Takahashi, 2000) and redescribed with necessary amendment. Furthermore, *Carthaginites yamashitai* sp. nov. is established on a fine specimen collected by M. Yamashita. The above two species occurred in the middle Cenomanian *Calycoceras* (*Newboldiceras*) *asiaticum* Zone in the Mikasa district of central Hokkaido.

(3) Morphologically and stratigraphically *Carthaginites* is intimately related to *Neostlingoceras* but differs in its smaller size, weaker ornamentation and especially by the deviated position of the siphuncle to the inner part of the whorl.

(4) In view of the peculiar characters as mentioned above, *Carthaginites* is presumed to have had a peculiar mode of life, but this ecological problem is not treated in this paper and left for further investigation.

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# The Anthracotheriidae (Mammalia; Artiodactyla) from the Eocene Pondaung Formation (Myanmar) and comments on some other anthracotheres from the Eocene of Asia

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**Abstract.** We reevaluate the classifications of the anthracotheres (Mammalia; Artiodactyla) from the latest middle Eocene Pondaung Formation (central Myanmar), mentioning other anthracotheres from the Eocene of Asia. The three anthracotheriid genera previously known from the Pondaung Formation, *Anthracothema*, *Anthracokeryx*, and *Anthracohyus*, are synonymized into *Anthracotherium*. As many as 13 species had been recognized in the Pondaung anthracotheres, but they are summarized into four species (*Anthracotherium pangan*, *Anthracotherium crassum*, *Anthracotherium birmanicum*, and *Anthracotherium tenuis*), based on the difference of  $M_1$  size ( $\sim$  body size). Dental morphology in each species indicates high variation, and the four species are not separable based on their dental morphology. The dental morphology of the Pondaung *Anthracotherium* species is distinct from that of other species and is the most primitive. In addition, the Pondaung *Anthracotherium* species are the oldest of the genus. The genus *Anthracotherium* might have originated and rapidly radiated around the Pondaung area during the latest middle Eocene. *Siamotherium pondaungensis* described from the Pondaung Formation as an anthracotheriid is synonymized to *Pakkokuhys lahirii* (Artiodactyla; Helohyidae).

**Key words:** Anthracotheriidae, *Anthracotherium*, Eocene, Myanmar, Pondaung Formation, systematics

## Introduction

The Anthracotheriidae is an extinct group of browsing suiform artiodactyls that achieved wide distribution across Eurasia, parts of Africa, and North America from the Eocene to Plio-Pleistocene periods (Black, 1978; Ducrocq, 1997; Kron and Manning, 1998). Their body size ranges from small, terrier-sized animals to beasts approaching the size of a hippopotamus (Black, 1978). Typical early anthracotheres have complete dentition and bunodont or bunoselenodont molars, five cusped upper molars without hypocone and four cusped lower molars without paraconid (Ducrocq *et al.*, 1996). Their low-crowned teeth and frequent occurrence in paleochannel deposits suggest habits and habitat similar to those of modern hippos (Kron and Manning, 1998).

The fossil record of anthracotheres is abundant and diverse throughout the world. In East Asia, they appeared from the middle Eocene and survived until the Plio-Pleistocene (Colbert, 1938; Ducrocq, 1997). In Europe, they appeared during the late Eocene and became extinct in the Miocene. In Africa, they evolved from the late Eocene to the Plio-Pleistocene (Black, 1978; Ducrocq, 1994a, 1997). In North America, they are recorded from the late middle Eocene to the early Miocene, but the fossil record of North American anthracotheres is neither particularly abundant nor very diverse (Kron and Manning, 1998).

In regard to the anthracotheres' phyletic relationships, traditionally, most researchers have considered that anthracotheres might have originated from a helohyid stock (Pilgrim, 1928, 1940; Coombs and Coombs, 1977; Ducrocq *et al.*, 1997) or from diacodexoid forms (Ducrocq, 1994b),

and that they might have been the ancestors of extant hippos because some types of anthracotheres are considered to have had a hippopotamid mode of life and a body structure similar to hippos (Black, 1978; Colbert, 1935; Gentry and Hooker, 1988; Thewissen *et al.*, 2001). According to molecular data (e.g., Nikaido *et al.*, 1999), hippopotamids comprise a monophyletic clade with cetaceans, so that anthracotheres might have originated from a stock of the [Cetacea + Hippopotamidae] clade (Rose, 2001). On the other hand, a few researchers (Pickford, 1983; but see Ducrocq, 1994b for discussion) suggested that hippopotamids could have originated not from an anthracothere stock but from a peccary one (Ducrocq, 1997).

In regard to regional origin, many researchers have considered that anthracotheres might have originated in East Asia during the Eocene (e.g., Pilgrim, 1928; Suteethorn *et al.*, 1988; Ducrocq, 1994a, 1999), because Eocene anthracotheres of East Asia are abundant and well diversified and because they show a primitive bunodont condition (Ducrocq, 1999).

The anthracotheres from the Eocene Pondaung Formation (Myanmar) are the first mammalian taxa in this formation to have been described (Pilgrim and Cotter, 1916). They are among the oldest anthracotheres in East Asia and consist of three genera and as many as 13 species (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938). Therefore, many studies have viewed the Pondaung anthracotheres in relation to the origin and early radiation of this group (e.g., Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Coombs and Coombs, 1977; Ducrocq, 1999).

Despite the richness of the fossil collections, the classification of the Pondaung anthracotheres has been problematic (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Holroyd and Ciochon, 1991). The taxonomic confusion on the Pondaung anthracotheres is likely to be due to their highly varied and primitive dental morphology.

In this paper, we reevaluate the classification of the Pondaung anthracotheres based on previously described fossil materials (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938) and new collections. We then also discuss classifications of some other Eocene anthracotheres of East Asia in relation to the revision of the classification of the Pondaung anthracotheres.

#### Institutional abbreviations

AMNH = American Museum of Natural History, New York, USA; CM = Carnegie Museum of Natural History, Pittsburgh, USA; BMNH = The Natural History Museum (formerly British Museum of Natural History), London, United Kingdom; DMR = Department of Mineral Resources, Bangkok, Thailand; GSI = Geological Survey of

India, Kolkata, India; IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; NSM = National Science Museum, Tokyo, Japan; UCMP = Museum of Paleontology, University of California, Berkeley, USA.

#### Materials

The new collections of Pondaung anthracotheres used here were discovered in 1997 by Myanmar researchers (Pondaung Fossil Expedition Team, 1997; Takai *et al.*, 1999), and in 1998 (November) and 1999 (November) by Myanmar-Japan joint team (Takai *et al.*, 2000, 2001; Egi and Tsubamoto, 2000; Tsubamoto *et al.*, 2000a, b, 2001, 2002; Shigehara *et al.*, 2002; Gebo *et al.*, in press). These new fossil materials are stored in the National Museum of the Union of Myanmar (Yangon, Myanmar). They are serially catalogued under NMMP-KU specimen numbers. NMMP stands for National Museum, Myanmar, Paleontology; and KU for Kyoto University (Japan). The dental measurements used here are listed in the Appendix.

#### Geologic setting

The Pondaung Formation is distributed in the western part of central Myanmar (Figure 1). The Pondaung Formation overlies and partially interfingers with the middle Eocene Tabyin Formation, and is conformably overlain by the late Eocene Yaw Formation (Stamp, 1922; Bender, 1983; Aye Ko Aung, 1999). The Pondaung Formation consists of alternating mudstone, sandstone, and conglomerate, and is subdivided into the "Lower" and "Upper" Members (Aye Ko Aung, 1999). The "Lower Member" is dominated by greenish pebbly sandstone and mudstone and contains only a few fossil leaf fragments in its upper part (Aye Ko Aung, 1999). The "Upper Member" is dominated by fine- to medium-grained sandstone and variegated mudstone and contains many terrestrial mammalian and other vertebrate fossils that indicate a freshwater environment (Colbert, 1938; Bender, 1983; Aye Ko Aung, 1999; Aung Naing Soe, 1999; Aung Naing Soe *et al.*, 2002). Its mammalian fauna and the fission-track age of the "Upper Member" ( $37.2 \pm 1.3$  Ma) indicate a latest middle Eocene age (Tsubamoto *et al.*, 2002).

#### Previous studies on Pondaung anthracotheres

Pilgrim and Cotter (1916) first described three genera (*Anthracohyus*, *Anthracotherium*, and *Anthracokeryx*) and seven species of anthracotheres from the Pondaung Formation. Pilgrim (1928) revised the Pondaung anthracotheres into three genera (*Anthracohyus*, *Anthracothema*, and *Anthracokeryx*) and 13 species, describing new



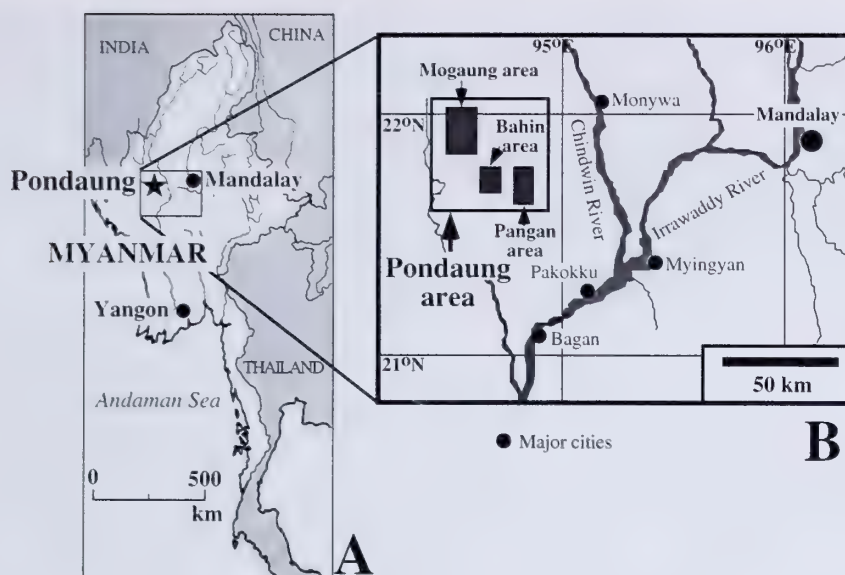


Figure 1. A. Map of Myanmar showing the location of the Pondaung area. B. Map of the Pondaung area showing the location of the three main regions of fossil localities.

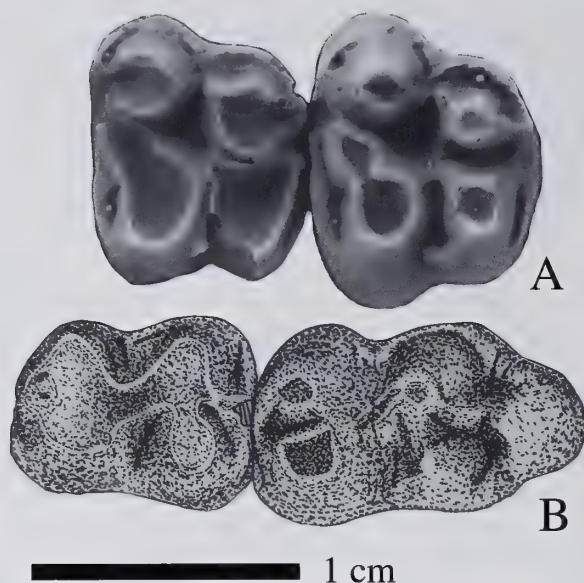
materials. Colbert (1938) reviewed the Pondaung anthracotheres, and recognized the same three genera as Pilgrim (1928) and seven to nine species, also describing new materials. Thus, in the Pondaung Formation, the three anthracothere genera *Anthracohyus*, *Anthracothema*, and *Anthracokeryx* have been traditionally recognized. All these three genera were established based on the material from the Pondaung Formation. Most of the anthracothere materials collected from the Pondaung Formation have been assigned to *Anthracothema* or *Anthracokeryx*, whereas remains of *Anthracohyus* have been very rare.

*Anthracohyus* was established by Pilgrim and Cotter (1916) and was characterized particularly by the absence or very feeble development of the styles on the upper molars. Originally, this genus included three species, that is, *Anthracohyus choeroides*, *Anthracohyus rubricae*, and *Anthracohyus palustris*. Subsequently, the latter two species were moved to a new genus *Anthracothema* as determined by Pilgrim (1928). This classification is followed by Colbert (1938). The only remaining species in the genus *Anthracohyus*, *A. choeroides*, was characterized by the conical cusps on its molars, by the absence or very feeble development of the molar styles, and by the mesiodistal diameter of the upper molar being shorter on the buccal side than on the lingual side (Colbert, 1938).

*Anthracothema* was established by Pilgrim (1928). Four species of the Pondaung anthracotheres described by Pilgrim and Cotter (1916) were referred to this genus: *Anthracohyus rubricae*, *Anthracohyus palustris*, *Anthracotherium pangan*, and *Anthracotherium crassum*. All

these species were renamed by Pilgrim (1928) as *Anthracothema rubricae*, *Anthracothema palustre*, *Anthracothema pangan*, and *Anthracothema crassum*, respectively. Afterwards, *A. palustre* and (questionably) *A. crassum* were synonymized to *A. pangan* by Colbert (1938). Therefore, two (or three) species of the Pondaung *Anthracothema* were still recognized by him. The genus *Anthracothema* was characterized by its larger size, weaker molar styles, and its more conical molar cusps than those of *Anthracokeryx* from the Pondaung Formation (Pilgrim, 1928; Colbert, 1938). Recently, *Anthracothema* was synonymized to *Anthracotherium* by Ducrocq (1999).

*Anthracokeryx* was erected by Pilgrim and Cotter (1916). They described two species of *Anthracokeryx*, *Anthracokeryx birmanicus* and *Anthracokeryx tenuis*. Pilgrim (1928) then described six more species of this genus, namely *Anthracokeryx hospes*, *Anthracokeryx bambusae*, *Anthracokeryx myaingensis*, *Anthracokeryx ulnifer*, *Anthracokeryx moriturus*, and *Anthracokeryx? lahirii*. Colbert (1938) later on recognized four to six species of the Pondaung *Anthracokeryx*. The genus *Anthracokeryx* was characterized by its smaller size, better marked molar styles, and its more crescentic (selenodont) molar cusps than *Anthracothema* and *Anthracohyus* from the Pondaung Formation (Pilgrim, 1928; Colbert, 1938). On the other hand, the taxonomic validity of keeping *Anthracokeryx? lahirii* in the Anthracotheriidae was discussed by both Pilgrim (1928) and Colbert (1938). Recently, this species was referred to the Helohyidae (Artiodactyla) and renamed *Pakkokuhyus lahirii* by Holroyd and Ciochon (1995).



**Figure 2.** Comparison of *Siamotherium pondaungensis* and *Pakkokuhyus lahirii*. **A.**  $M^{2-3}$  of the type of *Siamotherium pondaungensis* [NMMP-KU 0039 (Kdw 6): a right maxillary fragment with  $M^{2-3}$ ] in occlusal view (reversed). **B.**  $M_{2-3}$  of the type of *Pakkokuhyus lahirii* (GSI B-766: a right mandibular fragment with  $M_{1-3}$ ) in occlusal view.

### On *Siamotherium pondaungensis*

Based on a right maxillary fragment with  $M^{2-3}$  (Kdw 6 = NMMP-KU 0039; Figure 2A) from the Pondaung Formation, *Siamotherium pondaungensis* was described by Ducrocq *et al.* (2000) as a new species of *Siamotherium* (Anthracotheriidae). *Siamotherium* was known only from the Krabi basin, the late Eocene of Thailand (Suteethorn *et al.*, 1988; Ducrocq, 1999). However, the dentition displayed by the unique material of *S. pondaungensis* matches that of *Pakkokuhyus lahirii* (Helohyidae) (Figure 2B) described from the Pondaung Formation by Pilgrim (1928) and Holroyd and Ciochon (1995) based on a right mandibular fragment with  $M_{1-3}$ . Ducrocq *et al.* (2000) did not compare *S. pondaungensis* with *P. lahirii*. Although the upper dentition of *P. lahirii* has never been described, we believe that this upper dental material described as *S. pondaungensis* should be referred to *P. lahirii* rather than to another taxon because (1) the upper molars of *S. pondaungensis* are conical, bunodont, and brachyodont mo-

lars, like the lower molars of *P. lahirii*; (2) the sizes and cusp configurations of  $M^2$  and  $M^3$  of *S. pondaungensis* well match those of  $M_2$  and  $M_3$  of the type of *P. lahirii* (GSI B-766), respectively (e.g.,  $M^2$  protocone,  $M^3$  protocone, and  $M^3$  metaconule match  $M_2$  talonid basin,  $M_3$  talonid basin, and  $M_3$  hypoconulid basin, respectively) (Figure 2); (3) the upper dental morphology of *S. pondaungensis* is similar to that of helohyids, such as *Helohyus*, in having similar dental size, bunodont and conical cusps with enlarged metaconule, and no or vestigial styles; and additionally, (4) both *S. pondaungensis* and *P. lahirii* have been found only in the Pondaung Formation. Further discoveries of better materials are necessary to settle the classification, but following our observations on the dental materials, we treat *Siamotherium pondaungensis* as a junior synonym of *Pakkokuhyus lahirii* (Helohyidae) in this paper.

### Dental morphology and size variation of Pondaung anthracotheres and their classification

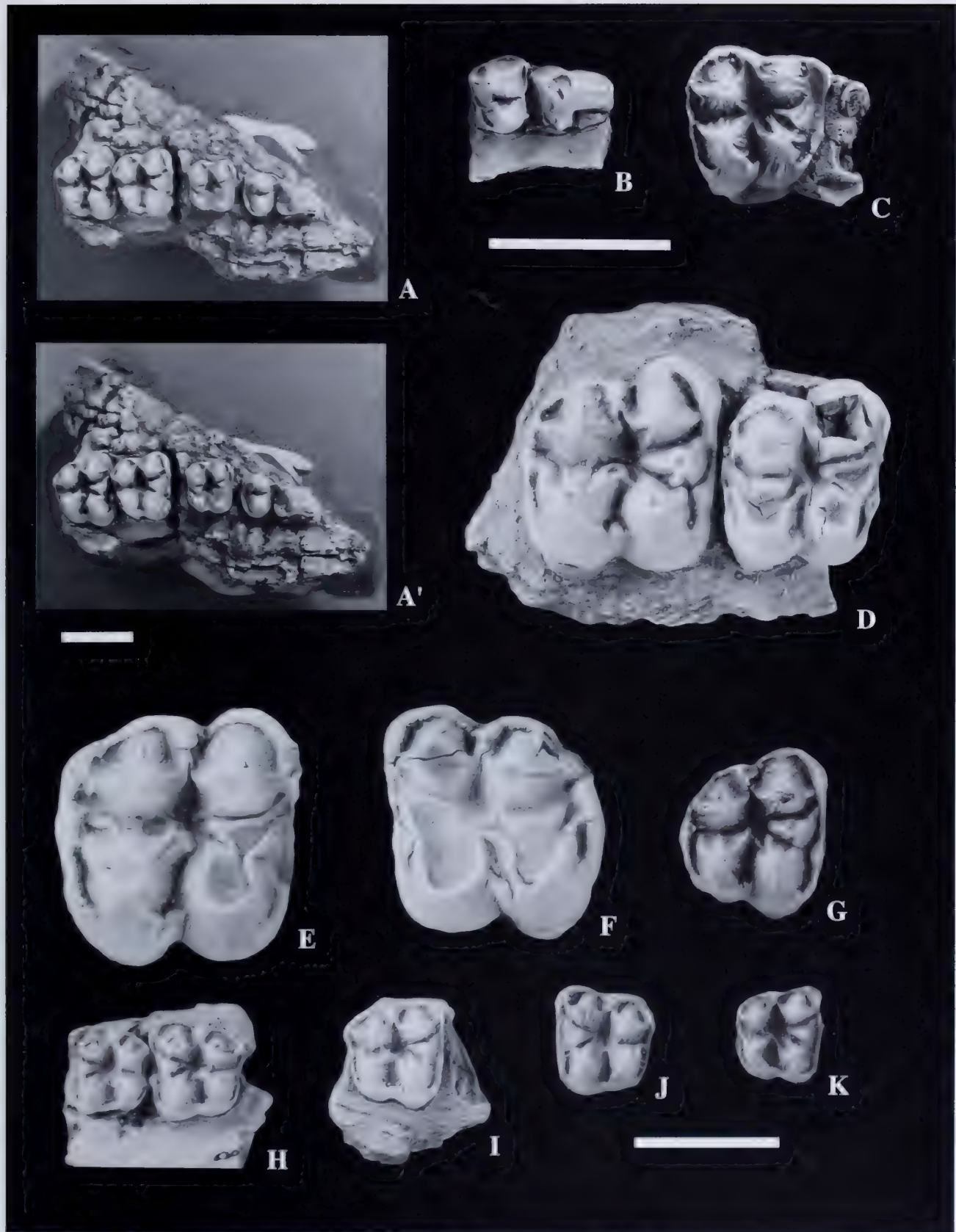
#### Generic status of *Anthracothema* and *Anthracokeryx*

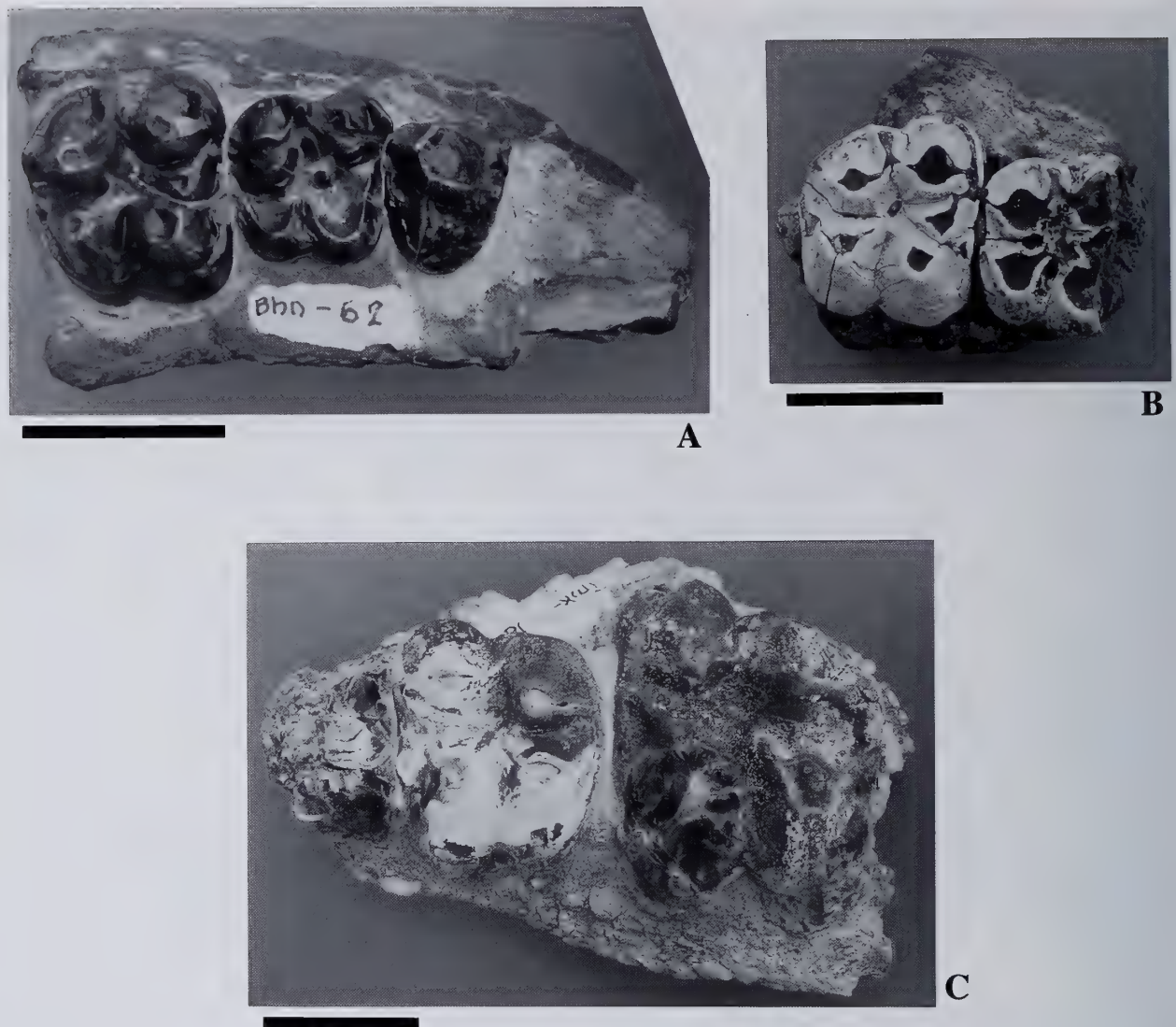
As mentioned above, after the review of Colbert (1938), the Pondaung anthracotheres have been classified into three genera, *Anthracohyus*, *Anthracothema*, and *Anthracokeryx*, and into as many as 13 species. This is because Colbert (1938) and earlier researchers (Pilgrim and Cotter, 1916; Pilgrim, 1928) recognized various dental morphologies among the Pondaung anthracotheres.

However, the differences in dental morphologies between two of the genera, *Anthracothema* and *Anthracokeryx*, in the Pondaung Formation are very subtle compared to other anthracotheriid taxa. In addition, these two genera have variations in selenodonty (crista development) and style development on the upper molars, which were the diagnostic characters for distinguishing them (Figures 3–5; Pilgrim and Cotter, 1916, plates 2–5; Pilgrim, 1928, plates 1–4; Colbert, 1938, figs. 41–52). Although *Anthracokeryx*, the smaller anthracothere group, generally has rather selenodont molars with better developed molar styles compared to *Anthracothema*, and although *Anthracothema*, the larger anthracothere group, generally has rather bunodont molars with less-developed styles compared to *Anthracokeryx*, the development of selenodonty and styles is variable. We examined all previously described materials of the Pondaung anthracotheres stored in AMNH and GSI, and recently collected materials in the National

➔ **Figure 3.** New upper dental materials of the Pondaung anthracotheres (*Anthracotherium*) in occlusal view (1). **A, A'.** NMMP-KU 0053, an right upper jaw with  $P^1$ - $M^1$  (stereo pair). **B.** NMMP-KU 0455, a right maxillary fragment with  $P^{2-4}$ . **C.** NMMP-KU 0327, a right mandibular fragment with  $dP^1$ . **D.** NMMP-KU 0056, a right maxillary fragment with  $M^{2-3}$ . **E.** NMMP-KU 0404, a right  $M^3$ . **F.** NMMP-KU 0411, a left maxillary fragment with  $M^3$ . **G.** NMMP-KU 0070, a right  $M^3$ . **H.** NMMP-KU 0382, a left maxillary fragment with  $M^{2-3}$  (or  $M^{1-2}$ ). **I.** NMMP-KU 0326, a right maxillary fragment with  $M^3$  (or  $M^2$ ). **J.** NMMP-KU 0379, a left  $M^3$ . **K.** NMMP-KU 0384, a right  $M^1$  (or  $M^2$ ). Scale bars = 2 cm (left middle scale corresponds to A, A', central upper scale corresponds to B–C, and right lower scale corresponds to D–K).







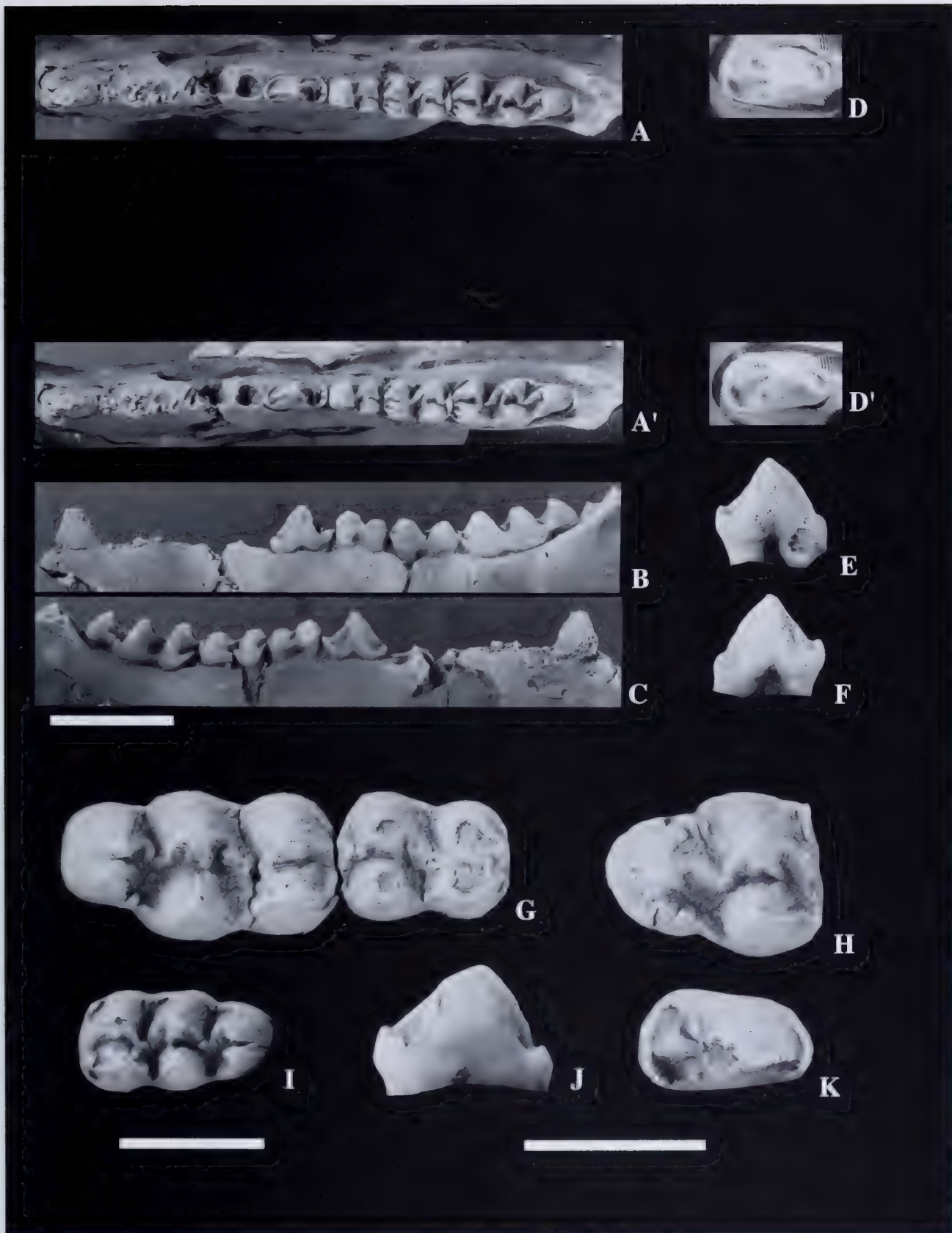
**Figure 4.** New upper dental materials of the Pondaung anthracotheres (*Anthracotherium*) in occlusal view (2). A. NMMP-KU 0413, a right maxillary fragment with  $P^4M^{1-2}$ . B. NMMP-KU 0216, a right maxillary fragment with  $M^{2-3}$ . C. NMMP-KU 0329, a left maxillary fragment with  $M^{1-3}$ . Scale bars = 2 cm.

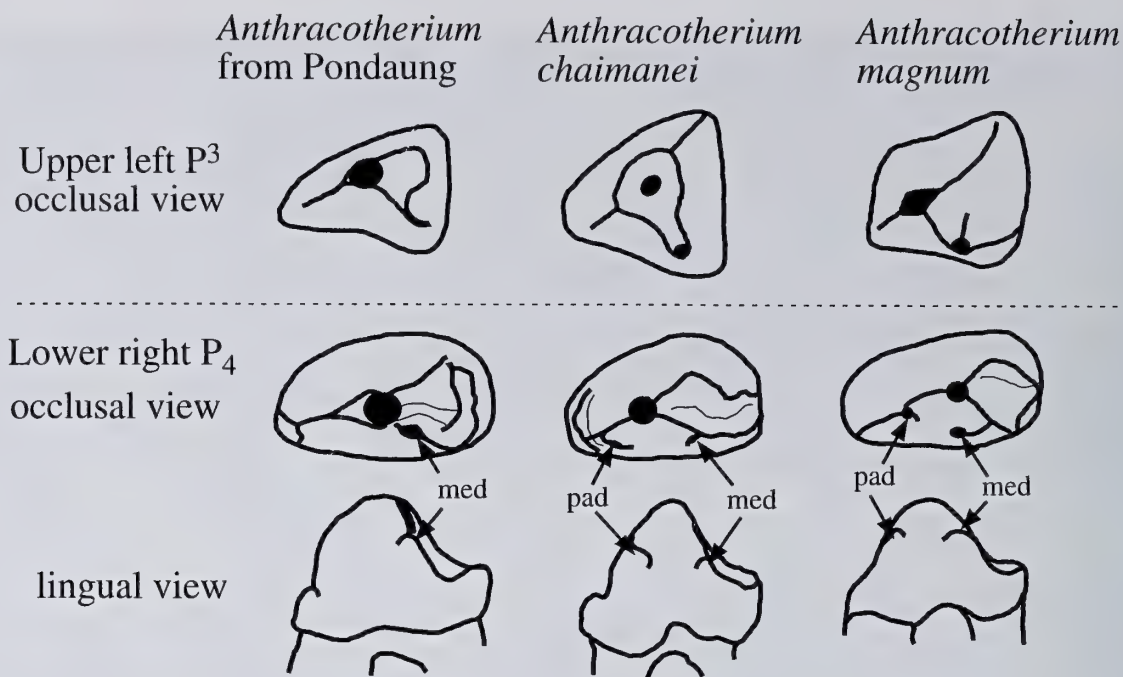
Museum of Myanmar. We did not find any critical differences in selenodonty and style development between the Pondaung *Anthracothema* and *Anthracokeryx*. Furthermore, we did not recognize any dental characteristics separating these two Pondaung anthracotheriid genera. For example, NMMP-KU 0056, a right maxillary fragment

with  $M^{2-3}$  (Figure 3D), has large dental size suggesting that it is referable to *Anthracothema*. However, the molar styles of this material are developed as well as or more than the small molar materials in Figure 3G–K, which may be referable to *Anthracokeryx*. Therefore, we conclude that the two genera are identical to each other.

➔ **Figure 5.** New lower dental materials of the Pondaung anthracotheres (*Anthracotherium*). A, A', B–C. NMMP-KU 0052, a right mandibular fragment with  $P_4M_3$ : A, A', occlusal view (stereo pair); B, lingual view; C, buccal view. D, D', E–F. NMMP-KU 0086, a left  $P_4$ : E, E', occlusal view (stereo pair); F, lingual view; G, buccal view. G. NMMP-KU 0330, a left mandibular fragment with  $M_{2-3}$ , in occlusal view. H. NMMP-KU 0419, a talonid part of left  $M_3$ , in occlusal view. I. NMMP-KU 0332, a right mandibular fragment with  $M_3$ , in occlusal view. J, K. NMMP-KU 0433, a right  $P_4$ : J, lingual view; K, occlusal view. Scale bars = 2 cm (left middle scale corresponds to A–C, A', and left lower scale corresponds to D–K, D', and right lower scale corresponds to J–K).







**Figure 6.** Schematic drawings of left  $P^3$  and right  $P_4$  of the Pondaung *Anthracotherium*, *Anthracotherium chaimanei*, and *Anthracotherium magnum*. Abbreviations: pad, paraconid; med, metaconid.

Furthermore, these two genera, *Anthracothema* and *Anthracokeryx*, are also similar to the genus *Anthracotherium* in regard to dental morphology (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938). Describing a new species of *Anthracotherium* from the late Eocene Krabi basin of Thailand, Ducrocq (1999) synonymized *Anthracothema* to *Anthracotherium*. He mentioned that the graduation observed in the style development of  $P^4$ – $M^3$ , in the robustness and orientation of  $P^3$ , and in the development of the lingual crests on the lower premolars among *Anthracothema pangan* from Pondaung, *Anthracotherium chaimanei* from Krabi, and *Anthracotherium monsvialense* from Europe probably indicates a direct relationship among these three taxa. We concur with Ducrocq's (1999) conclusion. In addition, we also synonymize *Anthracokeryx* to *Anthracotherium* in this paper because *Anthracokeryx* and *Anthracothema* are not separable from each other, as mentioned above. All these three genera have bunodont dentition, quite similar upper and lower molar morphologies to one another, and mesiodistally elongated simple  $P_4$ . No distinct characteristics of dental morphology distinguish the three genera.

#### Specific identification

Among the species of the genus *Anthracotherium*, definitive characteristics in upper and lower posterior premolars distinguish the Pondaung *Anthracotherium* species from

more progressive *Anthracotherium* species, such as *Anthracotherium chaimanei* from the late Eocene Krabi basin of Thailand and European *Anthracotherium* (e.g., *Anthracotherium magnum* from the Oligocene). These premolar characteristics indicate that the Pondaung *Anthracotherium* species resemble each other in their dental morphology more than they do any other species of this genus (Figures 3, 5, 6). The  $P^3$  in all materials of the Pondaung *Anthracotherium* has a mesiodistally elongated triangular outline in occlusal view with pre- and postprotocrista extending mesiodistally; whereas the  $P^3$  of *A. chaimanei* has a more mesiodistally compressed triangular outline with the pre- and postprotocrista running more diagonally, and that of *A. magnum* has a trapezoidal outline in occlusal view with pre- and postprotocrista running more diagonally (Figure 6; Ducrocq, 1999). The  $P_4$  in all materials of the Pondaung *Anthracotherium* has a vestigial metaconid but does not have any trace of paraconid, whereas *A. chaimanei* and *A. magnum* have both tiny paraconid and metaconid (Figure 6). The  $P^4$  in all materials of the Pondaung *Anthracotherium* is less selenodont and has much weaker styles than those in the  $P^4$  of *A. magnum* and *A. chaimanei*, as mentioned by Ducrocq (1999). Also, the development of the lingual crests on the lower premolars of the Pondaung *Anthracotherium* is weaker (Ducrocq, 1999). In such premolar morphologies, there are no critical characteristics that distinguish any group



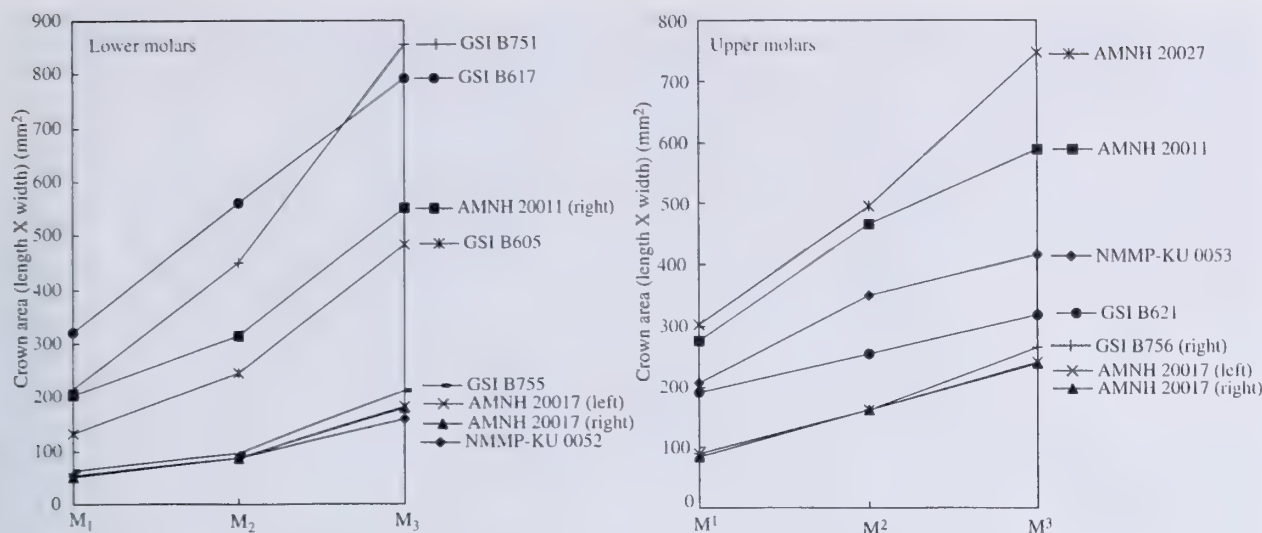


Figure 7. Size change (line chart) of upper and lower molars of the Pondaung anthracotheres in each individual.

among the Pondaung *Anthracotherium*. In addition, although there are individual variations, the Pondaung *Anthracotherium* species are distinct from other *Anthracotherium* species in having such molar morphologies as weaker selenodonty and weaker development of styles (Figures 3–5). These characteristics indicate that the Pondaung *Anthracotherium* species possess the most primitive dentition within the genus (Ducrocq, 1999).

Similar to the case of the dental morphology, the dental sizes of the Pondaung anthracotheres are highly variable. Figure 7 shows the line chart of the molar areas (width  $\times$  length) in individuals of the Pondaung anthracotheres. The size of  $M_1$  relative to  $M_2$  and  $M_2$  relative to  $M_3$  in a single individual is not constant among the Pondaung anthracotheres. For example,  $M_1$  in GSI B751 is much smaller than in GSI B617, while  $M_3$  in the former is rather larger than in the latter. This kind of variation shown in Figures 7 can be explained by individual variation and cannot be attributed to specific differences, as mentioned below.

The dental sizes of each tooth class of all the Pondaung anthracothere materials are also highly variable (Figures 8, 9). For example, the size of smallest  $M^3$  is about 15 mm in width and 14 mm in length, while that of largest  $M^3$  is about 45 mm in width and 39 mm in length (Figure 8). Such size differences do not support the idea that the Pondaung anthracotheres consist of one species. However, this distributional pattern of the dental size supports the argument that these animals belong to the same taxonomic category (that is, genus) because the scatter plots of the mesiodistal length and buccolingual width of  $P^3_1$ – $M^3_1$  are easily fitted to a straight-line by simple regression

(Figures 8, 9).

Among the dental size distributions (Figures 8, 9), it is noteworthy that the  $M_1$  size can be more readily divided into four groups than the other tooth classes. In general, the first molars are the first of the adult dentition to erupt and express less size variation among the adult dentition. A number of extant herbivores, including both browsing and grazing forms and certain species of hippos and suids, compensate for tooth wear by sequential or delayed tooth eruption (Kron and Manning, 1998). As the anterior teeth (and/or teeth erupting earlier) wear out, the emerging last molars (typically enlarged) take a progressively greater role in food comminution, resulting in no net loss of feeding efficiency (Kron and Manning, 1998). Thus, the teeth erupting later (posterior molars and premolars) are considered to express much wider dental size variations than do first molars in each species. In particular, lower first molars ( $M_1$ ) have been considered to express less size variation compared to upper first molars ( $M^1$ ), and to correlate very closely to the body size of mammals compared to other tooth classes (Gingerich, 1974; Gingerich and Schoeninger, 1979; Legendre, 1986, 1989; Conroy, 1987; Legendre and Roth, 1988; Dagosto and Terranova, 1992; Bown *et al.*, 1994).

Therefore, the distributional pattern of  $M_1$  size ( $\sim$  body size) in the Pondaung anthracotheres (Figure 9) suggests that the Pondaung anthracotheres can be divided into four subgroups within a single taxonomic group, that is, four species within a single genus, although a very high degree of size variation exists particularly in the posterior molars.

In relation to the specific classification of the Pondaung anthracotheres, we should mention here one dental charac-

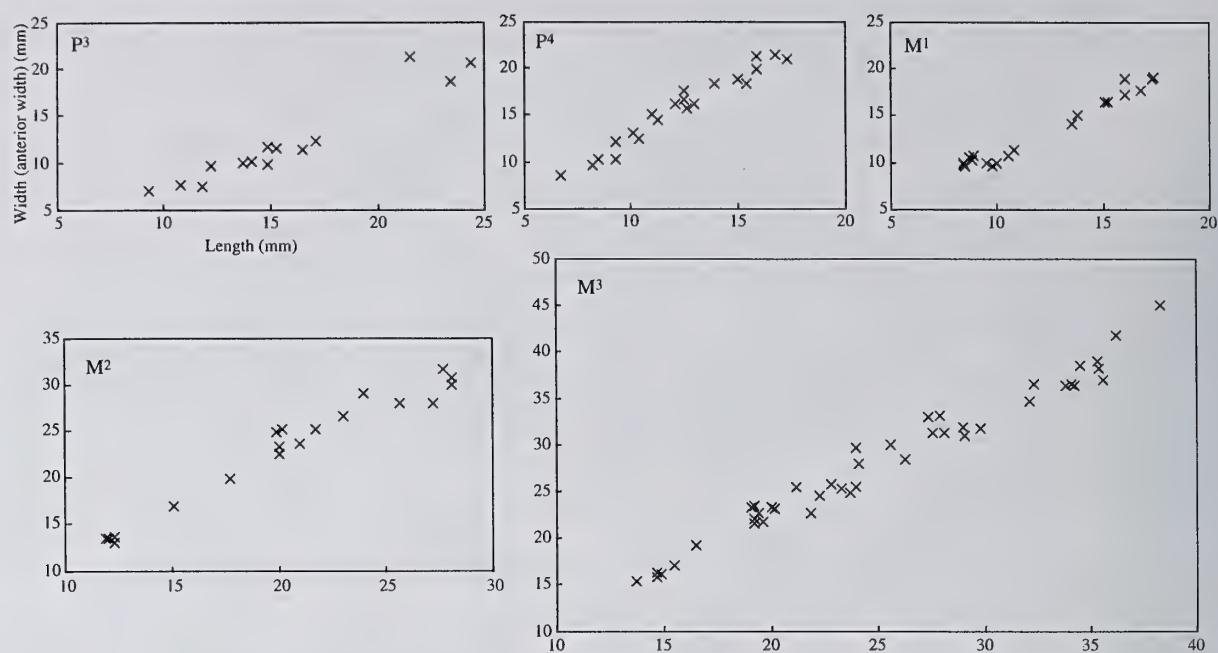


Figure 8. Size distribution of P<sup>3-4</sup> and upper molars of the Pondaung anthracotheres.

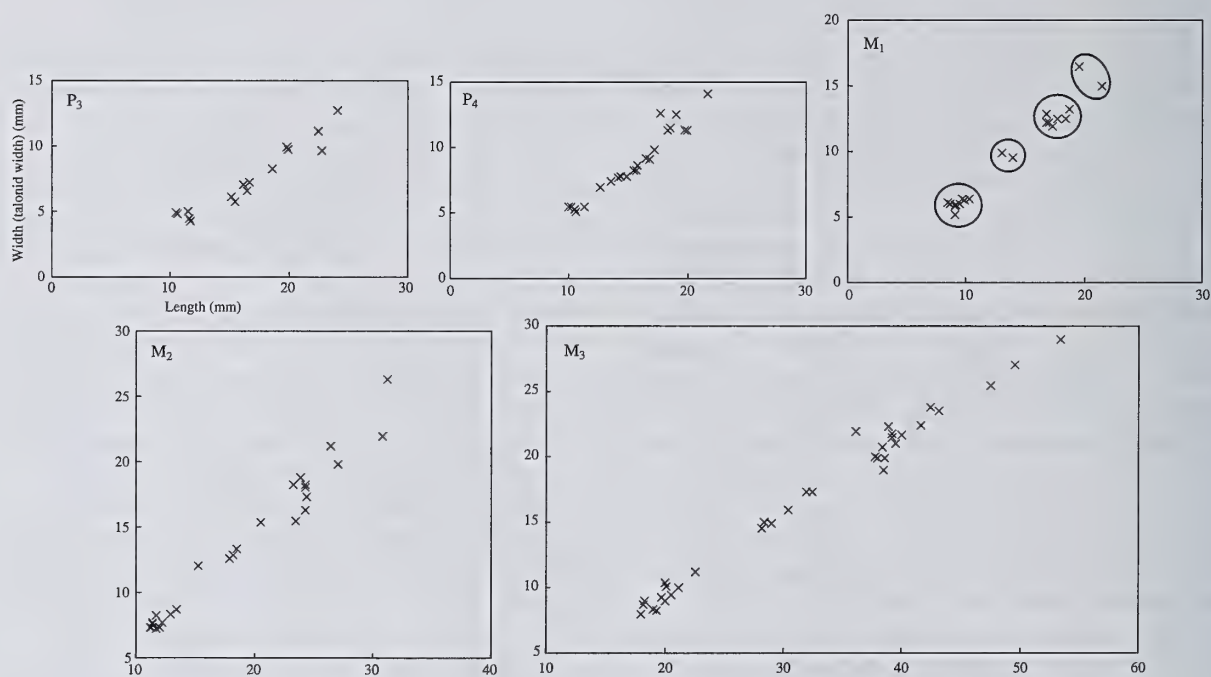
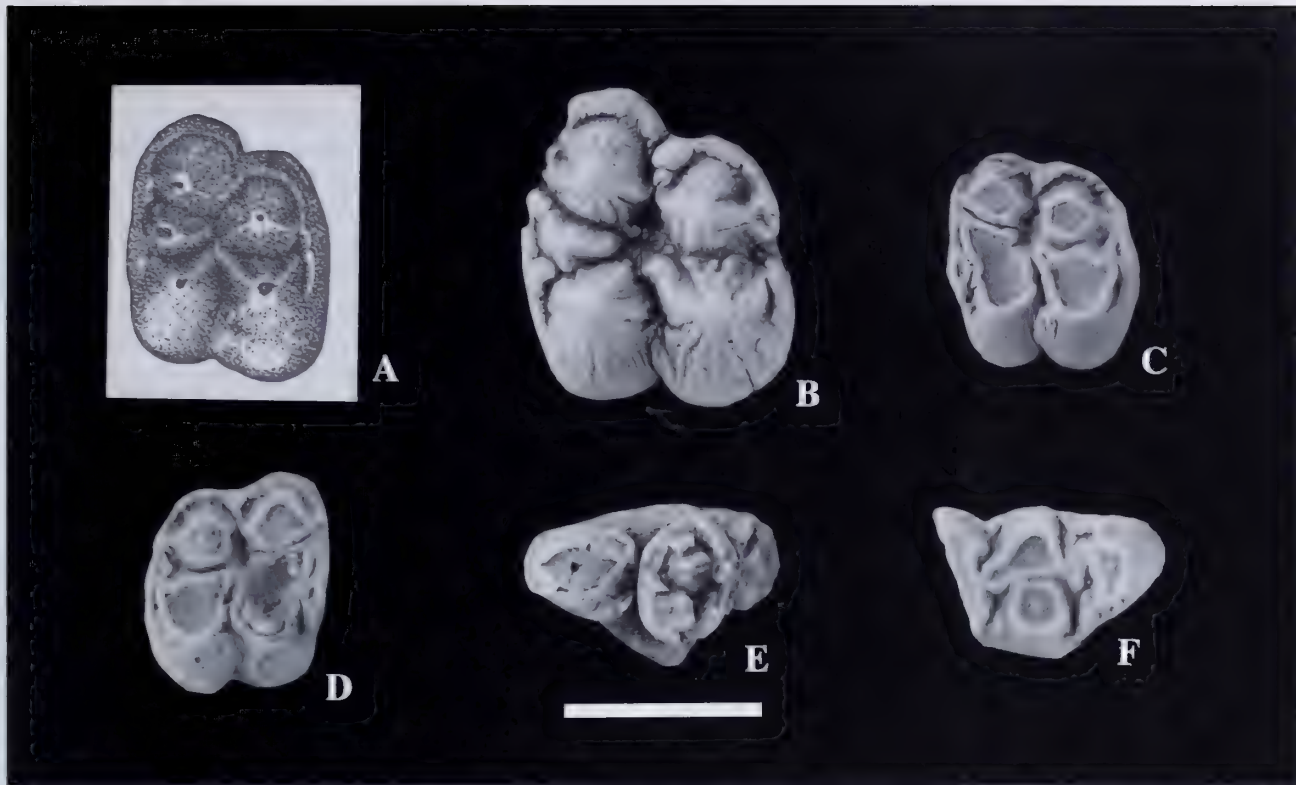


Figure 9. Size distribution of P<sub>3-4</sub> and lower molars of the Pondaung anthracotheres.





**Figure 10.** The Pondaung anthracothere materials of *Anthracohyus*-type in occlusal view. A. GSI B603 (holotype of *Anthracohyus choeroides*), a left  $M^1$ . B. NMMP-KU 0452, a left  $M^1$ . C. NMMP-KU 0454, a left  $M^1$ . D. NMMP-KU 0453, a right  $M^1$ . E. NMMP-KU 0500, a left maxillary fragment with  $P^{3-4}$ . F. NMMP-KU 0475, a right  $M_3$ . Scale bar = 2 cm.

teristic of  $M_3$ . Pilgrim (1928) distinguished the two small Pondaung anthracotheres, *Anthracokeryx ulnifer* and *Anthracokeryx myaingensis*, from one another on the basis of the morphology of the hypoconulid on  $M_3$ ; the former has a single cusp at the hypoconulid region on  $M_3$ , whereas the latter has a double cusp. Although most of the Pondaung anthracotheres have a double cusp at the hypoconulid region on  $M_3$ , the buccal of which is always larger and more distinct than the lingual one, the development of the lingual one is highly variable among all the examples of  $M_3$  in the Pondaung anthracotheres. For example, the lingual cusp in the hypoconulid on  $M_3$  is almost as large as the buccal one in NMMP-KU 0330 (Figure 5G), whereas it is very small and faint in NMMP-KU 0419 (Figure 5H). We consider this difference to be individual variation, not a specific characteristic.

#### Status of *Anthracohyus*

We also synonymize the remaining genus among the Pondaung anthracotheres, *Anthracohyus*, to *Anthracotherium*. Although *Anthracohyus* has unique dental structures in the upper molars (GSI B603, Figure 10A) (Pilgrim and Cotter, 1916; Pilgrim, 1938; Colbert, 1938),

the basic structures of its upper molars are referable to those of the Pondaung *Anthracotherium* (Figures 3, 4). Furthermore, the lower dental material of *Anthracohyus choeroides*, GSI B605 (a right mandibular fragment with complete dentition) (Pilgrim and Cotter, 1916, pl. 2, figs. 3, 3a-e, 4, 4a-e), is identical to that of *Anthracokeryx birmanicus* from the Pondaung Formation (Pilgrim, 1928, pl. 4, fig. 5; Colbert, 1938, fig. 45); there is no morphological or size distinction among the lower dental materials of the two species.

On the other hand, there are a few new specimens whose dental morphologies seem to be identical to that of *Anthracohyus* (Figure 10B-F): NMMP-KU 0452 (a left  $M^1$ ), 0453 (a right  $M^1$ ), 0454 (a left  $M^1$ ), 0475 (a right  $M_3$ ), and 0500 (a left maxillary fragment with  $P^{3-4}$ ) [the latter four specimens (NMMP-KU 0453, 0454, 0475, and 0500) probably belong to the same individual]. The upper molars among these (NMMP-KU 0452, 0453, 0454) have characteristics of *Anthracohyus*: very conical cusps, no or very vestigial styles on the upper dentition, and mesiodistally shorter buccal margins than the lingual one on the upper molars. The three examples of  $M^1$ , GSI B603 (type of *Anthracohyus choeroides*) (length: 21.2 mm;

width: 25.4 mm), NMMP-KU 0452 (length: 27.9 mm; width: 33.0 mm), and NMMP-KU 0453 (length: 19.6 mm; width: 21.8 mm), are separately scattered in the same linear size-distributional pattern prevalent among the Pondaung anthracotheres (Figure 6). Although these three specimens are not  $M_1$  and are considered to have relatively great size variation, they may be referred to the second largest, largest, and second smallest groups among the four groups of the Pondaung anthracotheres mentioned above, respectively, according to their sizes. Therefore, this size-distributional pattern also suggests that these *Anthracohyus*-type materials express one of the variations among the Pondaung anthracotheres, that is, species of *Anthracotherium*.

In conclusion, taking the variations of molar morphology (particularly development of upper molar styles) and size of the Pondaung anthracotheres into consideration (Figures 3–5), we interpret the dental morphology of *Anthracohyus* as one of the unusual individual variations of the Pondaung *Anthracotherium*. Otherwise, a multiplicity of species (of *Anthracothema*, *Anthracokeryx*, and *Anthracohyus*) which are morphologically and phylogenetically very close to one another, have to be maintained in a single fossil fauna (the Pondaung fauna). Such a situation seems unreasonable.

### Classification

To review, we synonymize all the genera of the Pondaung anthracotheres (*Anthracothema* Pilgrim, 1928, *Anthracokeryx* Pilgrim and Cotter, 1916, and *Anthracohyus* Pilgrim and Cotter, 1916) to *Anthracotherium* Cuvier, 1822. We group the Pondaung *Anthracotherium* materials into four species on the basis of  $M_1$  size ( $\sim$  body size). Materials lacking  $M_1$  are tentatively assigned to one of the four species based on the sizes of available teeth (Appendix).

There is a possibility that the larger two and smaller two of the four species might in fact be sexual dimorphic pairs as implied by Holroyd and Ciochon (1991). Most anthracotheres show a moderate amount of sexual dimorphism, but it is expressed by the canines: the individuals adjudged to have been male have larger canines than do the females (Kron and Manning, 1998). However, the fossil materials of the Pondaung anthracotheres are too poor to evaluate distribution of canine size, so there is no evidence to confirm that the larger two and smaller two represent male-and-female of sexually dimorphic species. Also, no critical difference in canine size relative to  $M_1$  is observed among the currently available materials. Therefore, we treat these four groups of the Pondaung *Anthracotherium* as four species in this paper.

Although the specific nomenclature of the Pondaung anthracotheres has been very complicated as mentioned above (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert,

1938), the following four species names can be retained based on the rule of priority: largest species, *Anthracotherium pangan* Pilgrim and Cotter, 1916; second largest species, *Anthracotherium crassum* Pilgrim and Cotter, 1916; second smallest species, *Anthracotherium birmanicum* (Pilgrim and Cotter, 1916); and smallest species, *Anthracotherium tenuis* (Pilgrim and Cotter, 1916). The possibility remains that the larger two (*A. pangan* and *A. crassum*) and smaller two (*A. birmanicum* and *A. tenuis*) might each be combinable as a sexually dimorphic species.

### Concluding remarks

The dental morphological comparisons in this study indicate that the Pondaung anthracotheres consist of four species of one genus (*Anthracotherium*). Their dental morphology, such as selenodonta, development of styles, and premolar shapes, suggest that the four species are much more similar to one another than to any other species of *Anthracotherium* from other deposits, although the dental morphology trend seems to be highly variable within the Pondaung *Anthracotherium*. In addition, the group of Pondaung *Anthracotherium* species has the other following features: (1) it is the oldest among the genus; (2) in basic dental morphology, the Pondaung *Anthracotherium* are likely to be the most primitive among the genus; and (3) their fossil materials predominate in collections of the Pondaung mammal fauna, suggesting a dominant population size (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Tsubamoto, 2001). Therefore, it is suggested that: (1) the genus *Anthracotherium* originated and rapidly radiated around the Pondaung area during the latest middle Eocene, and (2) *Anthracotherium* migrated from southern East Asia to Europe during the latest middle to late Eocene (Ducrocq, 1995).

### Systematic paleontology

Order Artiodactyla Owen

Family Anthracotheriidae Leidy

Genus *Anthracotherium* Cuvier, 1822

*Synonyms*.—*Anthracohyus* Pilgrim and Cotter, 1916; *Anthracokeryx* Pilgrim and Cotter, 1916; *Anthracothema* Pilgrim, 1928.

*Type species*.—*Anthracotherium magnum* Cuvier, 1822.

*Included species from Europe*.—*Anthracotherium monsvialense* De Zigno, 1888; *Anthracotherium alsaticum* Cuvier, 1822; *Anthracotherium seckbachense* Kinkelin, 1884; *Anthracotherium illyricum* Teller, 1886; *Anthracotherium bumbachense* Stehlin, 1910; *Anthracotherium cuvieri* Gaudry, 1873; *Anthracotherium hippondeum* Rüttimeyer, 1857; *Anthracotherium valdense*



Kowalevski, 1876; *Anthracotherium dalmatinum* von Meyer, 1854. (after Ducrocq, 1999)

*Included species from Asia.*—*Anthracotherium bugtiense* Pilgrim, 1907 (*sensu* Pickford, 1987); *Anthracotherium silistrense* Pentland, 1828 (*sensu* Pickford, 1987); *Anthracotherium changlingensis* Zhao, 1993; *Anthracotherium chaimanei* Ducrocq, 1999; *Anthracotherium thailandicus* (Ducrocq, 1999) new combination; *Anthracotherium gungkangensis* (Qiu, 1977) new combination; *Anthracotherium verhoeveni* (von Koenigswald, 1967); *Anthracotherium pangan* Pilgrim and Cotter, 1916; *Anthracotherium crassum* Pilgrim and Cotter, 1916; *Anthracotherium birmanicum* (Pilgrim and Cotter, 1916) new combination; *Anthracotherium tenuis* (Pilgrim and Cotter, 1916) new combination.

*Revised diagnosis.*—Large- to small-sized bunodont and primitive anthracothere. Differs from selenodont and bunoselenodont anthracotheres, such as *Elomeryx* and *Bothriogenys*, in having much simpler premolars and less developed selenodonta. Differs from *Siamotherium* in having double premetacristid on the lower molars (there is no distinct outer metacristid on those of *Siamotherium*), much better developed molar styles, less lingually located molar metacone in relation to paracone, much less mesiodistally compressed  $M^3$ , and much better developed protocone compared to paracone on  $P^{3-4}$ . Differs from *Anthracosenex* in having mesially or mesiobuccally oriented outer premetacristid rather than buccally oriented in *Anthracosenex*. Differs from *Heptacodon* in having less developed  $P_4$  cristids, and in lacking such strongly developed and prominent styles on the upper molars as in *Heptacodon*, and molar postentocristid that runs distobuccally and links to posthypocristid making a V-shaped notch. Differs from *Microbunodon* in having more bunodont cusps, less developed cingulum, rather straight (not V-shaped) ectoloph on  $P^{3-4}$ , and mesiodistally longer  $P^3$ .

#### *Anthracotherium pangan* Pilgrim and Cotter, 1916

*Anthracotherium pangan* Pilgrim and Cotter, 1916, p. 59–60, pl. 4, figs. 1–3.

*Anthracothema pangan* (Pilgrim and Cotter, 1916). Pilgrim, 1928, p. 10–13, pl. 1, figs. 1–7; Colbert, 1938, p. 353–355, figs. 41–42.

*Anthracohyus rubricae* Pilgrim and Cotter, 1916 (in part), p. 55–57, pl. 2, fig. 5–6, pl. 3, fig. 1–2.

*Anthracothema rubricae* (Pilgrim and Cotter, 1916) (in part). Pilgrim, 1928, p. 14; Colbert, 1983, p. 356–358.

*Anthracotherium crassum* Pilgrim and Cotter, 1916 (in part), p. 60–61, pl. 4, fig. 4–5, 5a.

*Anthracothema crassum* (Pilgrim and Cotter, 1916) (in part). Pilgrim, 1928, p. 16–18; Colbert, 1938, p. 355–356.

*Anthracohyus palustris* Pilgrim and Cotter, 1916, p. 58, pl. 3, figs. 7–9.

*Anthracothema palustre* (Pilgrim and Cotter, 1916). Pilgrim, 1928, p. 14–16, pl. 2, figs. 8–10; Colbert, 1938, p. 355.

*Lectotype.*—GSI B619, a left maxillary fragment with  $M^{2-3}$  (Colbert, 1938).

*Revised diagnosis.*—Large-sized and one of the most primitive *Anthracotherium* species. The dental morphology is almost identical to other Pondaung *Anthracotherium* species (i.e., *A. crassum*, *A. birmanicum*, and *A. tenuis*). Differs from the other Pondaung *Anthracotherium* species in having larger  $M_1$ . Differs from more progressive *Anthracotherium*, such as *A. magnum*, *A. monsvialense*, *A. bugtiense*, and *A. chaimanei*, in having slightly less selenodont cusps, less developed styles, mesiodistally elongated triangular outline of  $P^3$  in occlusal view having mesiodistally (not diagonal to the tooth row) extending paracrista, less developed lower premolar cristids, and less molariform  $P_4$  lacking a trace of paraconid. Differs from *A. thailandicus* in having slightly lower tooth crown in the lower dentition, less selenodonta, and metaconid on  $P_4$ , and lacking paraconid on  $P_4$ . Differs from *A. silistrense* in having larger size and slightly lower  $P_{3-4}$ . Differs from *A. gungkangensis* in having larger size, slightly less developed selenodonta and styles, more rounded outline of upper molars in occlusal view, and slightly wider and shorter upper molars. Differs from *A. verhoeveni* in lacking hypertrophied metastyle on the distal face of  $M^3$ . Differs from *A. changlingensis* in being smaller.

#### *Anthracotherium crassum* Pilgrim and Cotter, 1916

*Anthracotherium crassum* Pilgrim and Cotter, 1916 (in part), p. 60–61, pl. 5, fig. 1.

*Anthracothema crassum* (Pilgrim and Cotter, 1916) (in part). Pilgrim, 1928, p. 16–18; Colbert, 1938, p. 355–356.

*Anthracohyus rubricae* Pilgrim and Cotter, 1916 (in part), p. 55–57, pl. 2, fig. 7, pl. 3, figs. 3–6, 5a.

*Anthracothema rubricae* (Pilgrim and Cotter, 1916) (in part). Pilgrim, 1928, p. 14, pl. 2, figs. 1–7; Colbert, 1983, p. 356–358, figs. 43–44.

*Anthracohyus choeroides* Pilgrim and Cotter, 1916 (in part), p. 52–55, pl. 2, figs. 1–2.

*Anthracokeryx moriturus* Pilgrim, 1928, p. 32, pl. 4, figs. 1–3; Colbert, 1938, p. 376–379, figs. 51–52.

*Holotype.*—GSI B615, a left maxillary fragment with  $M^{2-3}$ .

*Revised diagnosis.*—Second largest (medium-sized) Pondaung *Anthracotherium*. Differs from *A. pangan* in having smaller  $M_1$ . Differs from *A. birmanicum* and *A. tenuis* in having larger  $M_1$ .

***Anthracotheium birmanicum*** (Pilgrim and Cotter, 1916)

*Anthrakeryx birmanicus* Pilgrim and Cotter, 1916 (in part), p. 61–62, pl. 5, figs. 2, 4; Pilgrim, 1928, p. 18–19, pl. 4, figs. 5, 5a; Colbert, 1938, p. 360–362, fig. 45.

*Anthrakeryx hospes* Pilgrim, 1928, p. 29–30; Colbert, 1938, p. 362–363.

*Anthrachyus choeroides* Pilgrim and Cotter, 1916 (in part), p. 52–55, pl. 2, figs. 3–4, 3a–3e, 4a–4e.

**Holotype.**—GSI B621, a right maxillary fragment with  $P^3$ – $M^3$ .

**Revised diagnosis.**—Second smallest (medium-sized) Pondaung *Anthracotheium*. Differs from *A. pangan* and *A. crassum* in having smaller  $M_1$ . Differs from *A. tenuis* in having larger  $M_1$ .

***Anthracotheium tenuis*** (Pilgrim and Cotter, 1916)

*Anthrakeryx tenuis* Pilgrim and Cotter, 1916, p. 62–63, pl. 5, figs. 6–8; Colbert, 1938, p. 364.

*Anthrakeryx birmanicus* Pilgrim and Cotter, 1916 (in part), p. 61–62, pl. 5, figs. 3, 5.

*Anthrakeryx bambusae* Pilgrim, 1928, p. 29; Colbert, 1938, p. 363.

*Anthrakeryx myaingensis* Pilgrim, 1928, p. 30–31, pl. 3, figs. 4–7; Colbert, 1938, p. 364–365.

*Anthrakeryx ulnifer* Pilgrim, 1928, p. 19–29, pl. 3, figs. 1–3, pl. 4, fig. 6; Colbert, 1938, p. 365–375, figs. 46–50.

**Holotype.**—GSI B625 (a left maxillary fragment with  $M^{1-2}$ ) and GSI B626 (a left mandibular fragment with  $M_1$  and posterior part of  $dP_4$ ).

**Revised diagnosis.**—Smallest (small-sized) Pondaung *Anthracotheium*. Differs from other Pondaung *Anthracotheium* species in having smaller  $M_1$ . Further differs from *A. thailandicus* in lacking the high and ventrally salient mandibular symphysis under  $P_1$ , and in having longer diastema between  $P_2$  and  $P_3$ . Further differs from *A. silistrense* in having longer diastema in the anterior premolar dentition.

## Family Helohyidae Marsh

Genus ***Pakkokuhyus*** Holroyd and Ciochon, 1995***Pakkokuhyus lahirii*** (Pilgrim, 1928)

*Anthrakeryx? lahirii* Pilgrim, 1928, p. 32–33, pl. 4, figs. 4, 4a; Colbert, 1938, p. 379.

*Pakkokuhyus lahirii* (Pilgrim, 1928). Holroyd and Ciochon, 1995, p. 178–180, fig. 1A, B.

*Siamotherium pondaungensis* Ducrocq *et al.*, 2000, p. 756, fig. 2.

**Holotype.**—GSI B766, right mandibular fragment with  $M_{1-3}$ .

**Revised diagnosis.**—A helohyid having bunodont and conical cusps, lacking hypocone at least on  $M^{2-3}$  and paraconid at least on  $M_{2-3}$ . Differs from *Gobiohyus* and *Helohyus* in having more bunodont and conical cusps, a basally inflated crown, larger metaconule on  $M^3$ , entoconid slightly posterior to hypoconid and less pronounced ectoflexid on the lower molars, a continuous labial cingulid on  $M_3$ , shorter and less distinct hypoconulid loop on  $M_3$ , stronger labial cingulids on  $M_{1-2}$ , and absolutely and relatively greater mandibular depth, and in lacking trace of molar hypocone, lingual cingulum and styler cusps on the upper molars, and molar paraconid. Further differs from *Gobiohyus* in having relatively higher crowns and from *Helohyus* in having a stronger hypoconulid on the distal cingulid and in lacking accessory cusplids on the hypoconulid loop. Differs from *Progeniohyus* in having smaller dental size, larger hypoconulid on  $M_3$ , and labial cingulid on  $M_3$ , and in lacking paraconid on  $M_2$ . Differs from the possible raoellid *Haqueina* in having entoconid slightly posterior to hypoconid, a stronger hypoconulid on the distal cingulid, and weaker hypolophid and cristid obliqua, a weaker and less constricted hypoconulid loop and a single hypoconulid on  $M_3$ . Differs from anthracotheriids in having smaller dental size, more conical (less selenodont) cusps, straight hypolophid on the lower molars, and shorter hypoconulid loop on  $M_3$ , and in lacking a double premetacristid on the lower molars.

**Comments on some other Eocene anthracotheres from Asia**

We reappraise several Eocene anthracotheres from Asia in relation to the revision of the Pondaung anthracotheres. *Anthracotheuma* and *Anthrakeryx* have been also reported from other deposits in the Eocene of Asia. Because the Pondaung *Anthracotheuma* and *Anthrakeryx* are the types of the two genera and the two were referred to *Anthracotheium*, all species of *Anthracotheuma* and *Anthrakeryx* are referred to *Anthracotheium*, except for *Anthrakeryx sinensis* (including *Anthrakeryx dawsoni* and *Anthracotheuma minima*), *Anthrakeryx litangensis*, and *Anthracotheuma lijiangensis*.

*Anthrakeryx birmanicus*, *Anthrakeryx moriturus*, *Anthrakeryx* sp. (= *Anthrakeryx* sp. cf. *bambusae*), and *Anthracotheuma rubricae*, which are conspecific with one or another of the Pondaung anthracotheres, are recorded from the late Eocene Naduo Formation, Bose and Yongle basins, Guangxi, southern China (Chow, 1957; Tang *et al.*, 1974; Qiu, 1977; Russell and Zhai, 1987). The materials of these species are poor, so that for the time being we tentatively refer these materials to the same species as



*Anthracotherium* from the Pondaung Formation. We refer *Anthracothema rubricae* and *Anthracokeryx moriturus* to *Anthracotherium crassum*, *Anthracokeryx birmanicus* to *Anthracotherium birmanicum*, and *Anthracokeryx* sp. to *Anthracotherium* sp.

*Anthracokeryx gungkangensis* and *Anthracokeryx kwangsiensis* are recorded from the late Eocene Gongkang Formation, which overlies the Naduo Formation (Qiu, 1977). *Anthracokeryx kwangsiensis* is also recorded from the Naduo Formation (Zhao, 1993). Ducrocq (1999) mentioned that these two species likely correspond to only one form in terms of their very similar morphology and dimensions. Following his suggestion, we treat *Anthracokeryx kwangsiensis* as a junior synonym of *Anthracokeryx gungkangensis*. Therefore, both of these species are referred to *Anthracotherium gungkangensis*.

*Anthracokeryx sinensis* is recorded from the Heti (Yuanchu basin), Xiangshan (Lijiang basin, Yunnan), and Huangzhuang (Qufu, Shandong) formations of the middle Eocene of China (Zdansky, 1930; Xu, 1962; Shi, 1989; Zhong *et al.*, 1996). We think that *Anthracokeryx sinensis* is not a bunodont but a primitive bunoselenodont anthracothere, so that this species is not referable to *Anthracotherium* (bunodont anthracothere). The  $P_4$  of *Anthracokeryx sinensis* (Zdansky, 1930, pl. 1, fig. 18; Xu, 1962, p. 241, fig. 1-3a) is much more molarized than that of progressive *Anthracotherium* species, such as *Anthracotherium magnum*. It has a somewhat triangle-shaped trigonid in occlusal view and resembles that of bunoselenodont or selenodont anthracotheres. Also, the upper molars of *Anthracokeryx sinensis* reveal stronger selenodontology than those of *Anthracotherium*. In particular, the paracone of the upper molars of *A. sinensis* is much more selenodont than that of *Anthracotherium*. The selenodontology of the upper molars of *A. sinensis* also appears similar to that of bunoselenodont anthracotheres, such as *Bothriogenys*. Therefore, we consider that it is better to establish a new genus for *Anthracokeryx sinensis*.

We suspect that it is better to synonymize both *Anthracokeryx dawsoni* and *Anthracothema minima* to *Anthracokeryx sinensis*. First, *Anthracokeryx dawsoni* was described by Wang (1985) from the late middle Eocene Zhaili Member of the Heti Formation (Yuanchu basin, central China), which also yields *Anthracokeryx sinensis*. The material of *Anthracokeryx dawsoni* consists of a skull with upper dentition. This material (IVPP V7915) has very similar dental morphology and size to *Anthracokeryx sinensis* except for a few dental differences (Xu, 1962, pl. 1, fig. 2-3, 8, 2A-3A, pl. 2, fig. 2, 2A; Wang, 1985, p. 58, pl., 1); such subtle differences seem to be within the range of intraspecific variation. Second, *Anthracothema minima* was described by Xu (1962, p. 233, 244, pl. 1, fig. 1, 1A) from the late middle Eocene Rencun Member of the Heti

Formation, which also yields *Anthracokeryx sinensis*. *Anthracothema minima* consists of only one upper molar (IVPP V2661), which has conical cusps like that of the Pondaung *Anthracothema* and *Anthracohyus*. However, its overall dental morphology and size are similar to that of *Anthracokeryx sinensis*. Taking the case of the Pondaung anthracotheres mentioned above into consideration, it may be better to consider that *Anthracothema minima* is also not a distinct species but one of the variations of *Anthracokeryx sinensis*.

*Anthracokeryx litangensis* was described from the late Eocene to early Oligocene Gemusi basin of Litang County (Sichuan, China), based on a right mandibular fragment with  $P_4M_1$  and an astragalus by Zhong *et al.* (1996). Although its only preserved lower molar ( $M_1$ ) is heavily worn (Zhong *et al.*, 1996, p. 265, pl. 21, fig. 3), the lower molar is rather selenodont than bunodont, having more lingually oriented preparacristid and cristid obliqua than *Anthracotherium* and *Anthracokeryx sinensis*. Its  $P_4$  is mesiodistally elongated and with well-developed cristids, suggesting it is referable neither to *Anthracotherium* nor to *Anthracokeryx sinensis*. The dental morphology of *Anthracokeryx litangensis* is rather similar to that of selenodont anthracotheres, such as *Bothriodon*.

*Anthracokeryx thailandicus* was described from the late Eocene Krabi basin of Thailand by Ducrocq (1999). We refer this species to the genus *Anthracotherium* and introduce for it the new combination *Anthracotherium thailandicus*.

Ducrocq (1999, p. 125, pl. 14G) described an anthracotheriid left  $M^3$  (DMR TF2662) from the Krabi basin as *Anthracotheriinae* gen. et sp. indet. This material is morphologically similar to that of *Anthracohyus* from the Pondaung Formation (Ducrocq, 1999) and is similar to *Anthracotherium thailandicus* in size. Thus, DMR TF2662 might be one of the individual variations of *A. thailandicus*.

*Anthracokeryx* sp. from the middle Eocene Lizhuang Formation (Henan, central China) was described by Wang and Zhou (1982) based on a broken right upper molar. Although this material was not illustrated, Wang and Zhou (1982) mentioned its morphological similarity to upper molars of *Anthracokeryx sinensis*. Here, we tentatively refer this material to cf. *Anthracokeryx sinensis*.

Cf. *Anthracokeryx* sp. was cited in the early to early middle Eocene Kuldana Formation (Indo-Pakistan) by Gingerich *et al.* (1979) and Russell and Zhai (1987). It is only represented by BMNH 32168, a left  $M_3$ , which was referred to *Lammidhania wardi* (Anthracobunidae) by Gingerich (1977). However, the dental morphology of BMNH 32168 is identical  $M_3$  of bunoselenodont anthracotheres, such as *Bothriogenys*, and is definitely not referable to *Anthracokeryx* (= *Anthracotherium*). Besides,



BMNH 32168 may be from the overlying Murree Formation (Russell and Zhai, 1987). Therefore, the existence of an *Anthracokeryx* (*Anthracotherium*)-like anthracothere in the Kuldana Formation is highly doubtful.

Cf. *Anthracokeryx* sp. was cited also in the late middle Eocene Shara Murun Formation (Inner Mongolia, northern China) by Russell and Zhai (1987). The sole specimen of this form, AMNH 22090 (a right mandibular fragment with  $M_3$ ), was originally described as *Gobiohyus robustus* (Helohyidae) by Matthew and Granger (1925). The  $M_3$  of the specimen has three large and distinct cusps at the hypoconulid region and reveals a bilophodont structure, which have never been seen in anthracotheres. Therefore, the existence of an *Anthracokeryx* (*Anthracotherium*)-like anthracothere in the Shara Murun Formation is also highly doubtful.

*Anthracothema lijiangensis* was described from the middle Eocene Xiangshan Formation (Lijiang basin, Yunnan, southern China) by Zong *et al.* (1996). This species differs from *Anthracotherium* in having straight (not V-shaped) hypolophid, mesiodistally rather than mesiolingually oriented cristid obliqua, and no buccal premetacristid directed mesiobuccally on the lower molars (Zong *et al.*, 1996, p. 279, pl. 35, fig. 2). These characteristics demand rejection of a reference of *Anthracothema lijiangensis* to *Anthracotherium*. It may be better to establish a new genus for this species (*Anthracothema lijiangensis* is distinguished from *Anthracokeryx sinensis*). On the other hand, although the material of *Anthracothema lijiangensis* was referred to the Anthracotheriidae by Zong *et al.* (1996) and Huang (1999), this familial position of *A. lijiangensis* is also doubtful because the species have straight hypolophid and no trace of mesiobuccally-directed premetacristid on the lower molars, both which are not appropriate to the anthracotheriid diagnosis (Holroyd and Ciochon, 1995).

*Anthracotherium chaimanei* was originally reported as *Anthracothema* sp. cf. *A. pangan* from the Krabi basin of Thailand by Ducrocq *et al.* (1992). It was formally described by Ducrocq (1999).

*Anthracotherium verhoeveni* was originally described from Timor (Indonesia) (but see Ducrocq, 1996, p. 765) as *Anthracothema verhoeveni* by von Koenigswald (1967). It was referred to the genus *Anthracotherium* by Ducrocq (1999).

*Anthracotherium*? spp. were cited in the middle middle Eocene Lushi Formation (Henan, central China) by Chow *et al.* (1973). However, this report contained no illustration of their material. In addition, the mammalian fauna of the Lushi Formation, which was referred to the middle middle Eocene (Irdinmanhan East Asian Land Mammal Age) (Russell and Zhai, 1987), is much older than the latest middle Eocene Pondaung Formation including the oldest posi-

tive *Anthracotherium* species. Therefore, the presence of the genus *Anthracotherium* in the Lushi Formation is doubtful (Russell and Zhai, 1987).

*Heothema* is recorded from the late Eocene Naduo and Gongkang Formations (Bose and Yongle basins, Guangxi) and lower part of Yongning Formation (late Eocene or early Oligocene; Nanning basin, Guangxi) of southern China (Tang, 1978; Zhao, 1981, 1983, 1993). Although the genus *Heothema* was synonymized to *Anthracotherium* by Ducrocq (1999), this genus may be valid because: (1) the molars and  $P^4$  of *Heothema* are more selenodont than those of *Anthracotherium*; (2) crests on the lingual face of lower premolars in *Heothema* (Tang, 1978, pl. 3, fig. 1, 1A) are stronger than those in *Anthracotherium*; and (3)  $P_4$  of *Heothema* seems to be more molariform than that of *Anthracotherium*, having a somewhat triangularly-shaped trigonid outline in occlusal view (Tang, 1978, pl. 3, fig. 1). Judging from these morphological points, *Heothema* might be one of the primitive bunoselenodont anthracotheres. For specific division of *Heothema*, we follow the grouping by Ducrocq (1999, p. 121), who recognized two species, *Heothema bellia* and *Heothema chengbiensis*.

*Huananothema imparilica* was described as a new genus and species of the Anthracotheriidae by Tang (1978) based on an upper molariform tooth from the late Eocene Naduo Formation, which also yields *Heothema*. According to Tang (1978), the type and unique material of *Huananothema imparilica* (IVPP V4964) is an upper molar, and therefore this species is identified by its upper molar having an anterior buccolingual width less than its posterior buccolingual width, in contrast to other anthracotheres (in the upper molars of all other anthracotheres, the anterior buccolingual width is greater than the posterior buccolingual width). However, this feature in IVPP V4964 is a typical  $dP^4$  morphology of large anthracotheres as seen in DMR TF 2901, a right  $dP^4$  of *Anthracotherium chaimanei* from the Krabi basin of Thailand (Ducrocq, 1999, pl. 5, fig. B), and also in NMMP-KU 0327, an upper dental specimen of the Pondaung *Anthracotherium* (Figure 3C). Therefore, IVPP V4964 is  $dP^4$ , so that the diagnosis of *Huananothema imparilica* by Tang (1978) is invalid. By comparing its size and morphology with those of anthracotheres from the Naduo Formation, we consider that IVPP V4964 is a  $dP^4$  of *Heothema chengbiensis*. Therefore, we synonymize both the genus *Huananothema* and species *Huananothema imparilica* to genus *Heothema* and species *Heothema chengbiensis*, respectively.

The materials of *Probrachyodus* are poor. Russell and Zhai (1987, p. 130) mentioned that this genus may be inseparable from *Anthracokeryx* (that is, *Anthracotherium* or the same genus as *Anthracokeryx sinensis*). However, the upper molars of *Probrachyodus* show bunoselenodonty, so



that this species differs from *Anthracotherium*, which comprises bunodont anthracotheres. *Probrachyodus* is distinct from *Anthracokeryx sinensis* and also further from *Anthracotherium* in having more lingually procumbent molar paracone and metacone. Therefore, we consider this genus a valid one. *Probrachyodus panchiaoensis* was described from the middle Eocene Lumeiyi Formation (Yunnan, Lunan basin, southern China) by Xu (1962). *Probrachyodus?* sp. nov. was cited in the middle Eocene Dongjun Formation (Guangxi, southern China) by Ding *et al.* (1977).

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**Appendix.** Dental measurements (in mm) of the Pondaung *Anthracotherium* used in this paper (Figures 7–9). Abbreviations: L, anteroposterior length; W, buccolingual width; \*, estimate; [ ] (square bracket), the data are from the literature (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938).

## Upper dentition

Specimen number	Taxa	P3/ L	P3/ W	P4/ L	P4/ W	M1/ L	M1/ W	M2/ L	M2/ W	M3/ L	M3/ W
NMMP-KU 0053	<i>A. birmanicum</i>	14.1	10.1	10.4	12.5	13.8	15.0	17.7	19.8	19.2	21.6
NMMP-KU 0056	<i>A. sp. cf. A. crassum</i>							23.0	26.6	28.1	31.2
NMMP-KU 0066	<i>A. tenuis</i>					10.8	11.4				
NMMP-KU 0067	<i>A. sp. cf. A. crassum</i>			12.1	16.1						
NMMP-KU 0070	<i>A. birmanicum</i>									20.2	23.2
NMMP-KU 0071	<i>A. sp. cf. A. crassum</i>					15.1	16.4				
NMMP-KU 0074	<i>A. sp. cf. A. pangan</i>			13.9	18.3						
NMMP-KU 0081	<i>A. birmanicum</i>									19.2	23.4
NMMP-KU 0082	<i>A. birmanicum</i>									19.4	22.6
NMMP-KU 0083	<i>A. birmanicum</i>									19.1	23.3
NMMP-KU 0103	<i>A. pangan</i>			15.9	21.2						
NMMP-KU 0105	<i>A. sp. cf. A. crassum</i>			11.0	15.0						
NMMP-KU 0106	<i>A. sp. cf. A. birmanicum</i>	13.7	9.9								
NMMP-KU 0122	<i>A. sp. cf. A. birmanicum</i>	17.1*	12.2	12.5	16.6	15.2	16.5				
NMMP-KU 0128	<i>A. sp. cf. A. birmanicum</i>									21.9	22.7*
NMMP-KU 0215	<i>A. sp. cf. A. birmanicum</i>	14.9	11.6								
NMMP-KU 0216	<i>A. sp. cf. A. crassum</i>									24.1	28.0
NMMP-KU 0275	<i>A. pangan</i>									38.3	45.0
NMMP-KU 0284	<i>A. sp. cf. A. birmanicum</i>									23.3	25.3
NMMP-KU 0325	<i>A. tenuis</i>					10.5	10.7				
NMMP-KU 0328	<i>A. pangan</i>									35.6	37.0
NMMP-KU 0329	<i>A. pangan</i>							27.7	31.6	36.2	41.8
NMMP-KU 0379	<i>A. tenuis</i>									13.7	15.3
NMMP-KU 0380	<i>A. tenuis</i>					8.5	9.7				
NMMP-KU 0385	<i>A. tenuis</i>					8.4	9.8				
NMMP-KU 0387	<i>A. tenuis</i>					9.5	10.0				
NMMP-KU 0388	<i>A. tenuis</i>					10.0	10.0				
NMMP-KU 0389	<i>A. tenuis</i>					10.5	10.7				
NMMP-KU 0401	<i>A. sp. cf. A. birmanicum</i>									22.8	25.8
NMMP-KU 0403	<i>A. sp. cf. A. crassum</i>									29.1	30.9
NMMP-KU 0404	<i>A. sp. cf. A. pangan</i>									34.2	36.4
NMMP-KU 0407	<i>A. sp. cf. A. pangan</i>									34.1	36.5
NMMP-KU 0408	<i>A. pangan</i>							28.1	30.0		
NMMP-KU 0409	<i>A. sp. cf. A. crassum</i>									27.4	32.9
NMMP-KU 0410	<i>A. sp. cf. A. crassum</i>							20.2	25.1*	24.0	29.6
NMMP-KU 0411	<i>A. sp. cf. A. crassum</i>									29.8	31.7
NMMP-KU 0412	<i>A. pangan</i>									35.3	38.9
NMMP-KU 0413	<i>A. crassum</i>			12.6	15.7	16.8	17.7	21.0	23.6		
NMMP-KU 0414	<i>A. sp. cf. A. crassum</i>					17.4	19.1	25.7	28.0		
NMMP-KU 0452	<i>A. sp. cf. A. crassum</i>									27.9	33.0
NMMP-KU 0453	<i>A. birmanicum</i>									19.2	22.1
NMMP-KU 0454	<i>A. birmanicum</i>									19.6	21.8
NMMP-KU 0455	<i>A. tenuis</i>	9.3	7.0	6.7	8.5						
NMMP-KU 0459	<i>A. sp. cf. A. crassum</i>									25.6	29.9
NMMP-KU 0463	<i>A. sp. cf. A. birmanicum</i>									22.3	24.5*
NMMP-KU 0476	<i>A. sp. cf. A. pangan</i>			15.4	18.4						
NMMP-KU 0480	<i>A. pangan</i>			17.3	21*						
NMMP-KU 0500	<i>A. birmanicum</i>	12.2	9.7	10.1	13.1						
AMNH 20011	<i>A. crassum</i>	16.5*	11.3	11.3	14.5	16.0	17.3	20.0	23.3	23.7	24.8
AMNH 20015	<i>A. birmanicum</i>									20.0	23.3
AMNH 20017 (right)	<i>A. tenuis</i>					8.4	10.0	12.0	13.5	14.7	16.3
AMNH 20017 (left)	<i>A. tenuis</i>	10.8	7.6	8.2*	9.6	8.8	10.2	11.9	13.5	14.9	16.1
AMNH 20024	<i>A. crassum</i>							20.0*	22.5*	24.0*	25.5
AMNH 20027	<i>A. crassum</i>			12.5*	17.6	16.0	18.9	19.9	24.9	26.3	28.4
AMNH 32525	<i>A. crassum</i>			13.0	16.2	17.3*	18.9				
AMNH 32526	<i>A. pangan</i>							[24]	[29]	32.3	36.5



Specimen number	Taxa	P3/ L	P3/ W	P4/ L	P4/ W	M1/ L	M1/ W	M2/ L	M2/ W	M3/ L	M3/ W
GSI B603	<i>A. crassum</i>									21.2	25.4
GSI B604	<i>A. crassum</i>	15.6	11.2								
GSI B608	<i>A. pangan</i>	24.6	20.4								
GSI B609	<i>A. pangan</i>									32.8	34.8
GSI B610	<i>A. pangan</i>							26.3	30.3		
GSI B611	<i>A. crassum</i>			14.4	18.8						
GSI B615	<i>A. crassum</i> (type)							21.7	25.1	27.6	31.2
GSI B616	<i>A. pangan</i>			15.9	19.9						
GSI B618	<i>A. pangan</i>	24.2	19.3								
GSI B619	<i>A. pangan</i> (type)							27.1	30.0*	34.0	36.4
GSI B621	<i>A. birmanicum</i> (type)	14.6	9.6	9.3*	11.8	13.0*	14.0*	15.0	16.8	16.7	19.0
GSI B622	<i>A. tenuis</i>							12.1	12.9	14.6	15.6
GSI B625	<i>A. tenuis</i> (type)					9.7	9.5				
GSI B748	<i>A. pangan</i>	21.5*	21.2*	16.2	22.3						
GSI B750	<i>A. pangan</i>							[28.1]	[30.8]	36.4	38.4
GSI B752	<i>A. pangan</i>									33.4	39.8
GSI B756 (right)	<i>A. tenuis</i>	11.6	7.2	8.9	10.4	8.5	10.7	11.9	13.5	15.6	17.0
GSI B756 (left)	<i>A. tenuis</i>			9.2	10.4	8.9	10.7	12.3	13.5		
GSI B763	<i>A. crassum</i>									27.6*	30.0*

## Lower dentition\*

Specimen number	Taxa	P/3 L	P/3 W	P/4 L	P/4 W	M/1 L	M/1 W	M/2 L	M/2 W	M/3 L	M/3 W
NMMP-KU 0052	<i>A. tenuis</i>			10.6	5.1	9.1	5.8	12.0	7.3	19.0	8.3
NMMP-KU 0062	<i>A. sp. cf. A. crassum</i>							27.1	19.8		
NMMP-KU 0063	<i>A. tenuis</i>					9.1	5.9				
NMMP-KU 0077	<i>A. sp. cf. A. crassum</i>									43.1	23.5
NMMP-KU 0079	<i>A. sp. cf. A. birmanicum</i>	16.2	7.0								
NMMP-KU 0086	<i>A. sp. cf. A. crassum</i>			15.5	8.2						
NMMP-KU 0087	<i>A. sp. cf. A. crassum</i>									38.8*	22.3
NMMP-KU 0093	<i>A. tenuis</i>									18.2	8.7
NMMP-KU 0107	<i>A. tenuis</i>	11.5	5.0								
NMMP-KU 0113	<i>A. tenuis</i>			10.5	5.3						
NMMP-KU 0116	<i>A. sp. cf. A. birmanicum</i>			14.8	7.8			18.2*	12.9		
NMMP-KU 0125	<i>A. birmanicum</i>	15.5	5.7	13.5	7.4			17.9	12.6		
NMMP-KU 0263	<i>A. tenuis</i>									20.1	10.1
NMMP-KU 0267	<i>A. tenuis</i>					9.2	5.9	11.2	7.3		
NMMP-KU 0274	<i>A. crassum</i>	19.9	9.7	18.5	11.5	17.7*	12.5*				
NMMP-KU 0306	<i>A. sp. cf. A. pangan</i>	22.8	9.6								
NMMP-KU 0307	<i>A. sp. cf. A. pangan</i>			18.3	11.3						
NMMP-KU 0330	<i>A. crassum</i>							24.3	18.2	39.2	21.5
NMMP-KU 0331	<i>A. crassum</i>							24.4	17.3		
NMMP-KU 0332	<i>A. birmanicum</i>									28.2	14.5
NMMP-KU 0399	<i>A. tenuis</i>									19.3	8.2
NMMP-KU 0415	<i>A. sp. cf. A. crassum</i>									42.4	23.8
NMMP-KU 0417	<i>A. sp. cf. A. crassum</i>									40*	21.7
NMMP-KU 0418	<i>A. pangan</i>							31.2	26.3		
NMMP-KU 0421	<i>A. crassum</i>					17.3	11.9				
NMMP-KU 0422	<i>A. tenuis</i>							11.7	8.2	20.0*	10.4
NMMP-KU 0423	<i>A. tenuis</i>									18.3	9.0
NMMP-KU 0424	<i>A. crassum</i>									38.5	19.9
NMMP-KU 0426	<i>A. crassum</i>							23.3*	18.2*	39.5*	21.0*
NMMP-KU 0427	<i>A. sp. cf. A. crassum</i>									41.6	22.4
NMMP-KU 0429	<i>A. crassum</i>							24.3	16.3	37.7	20.0
NMMP-KU 0430	<i>A. birmanicum</i>	16.5	6.6	14.3	7.8						
NMMP-KU 0432	<i>A. sp. cf. A. crassum</i>			15.7	8.2						
NMMP-KU 0433	<i>A. pangan</i>			19.9	11.3						

Specimen number	Taxa	P/3 L	P/3 W	P/4 L	P/4 W	M/1 L	M/1 W	M/2 L	M/2 W	M/3 L	M/3 W
NMMP-KU 0434	<i>A. pangan</i>			17.7	12.6						
NMMP-KU 0435	<i>A. crassum</i>			16.8	9.1						
NMMP-KU 0457	<i>A. crassum</i>									38.4	19.0
NMMP-KU 0458	<i>A. tenuis</i>					9.9*	6.3	13.4	8.7		
NMMP-KU 0465	<i>A. tenuis</i>									22.6	11.2
NMMP-KU 0466	<i>A. tenuis</i>							12.2	7.7		
NMMP-KU 0468	<i>A. crassum</i>					18.4	12.5				
NMMP-KU 0470	<i>A. tenuis</i>							11.3	7.3	20.5	9.4
NMMP-KU 0478	<i>A. birmanicum</i>					10.3	6.4	12.9	8.3		
NMMP-KU 0505	<i>A. sp. cf. A. crassum</i>			15.8	8.6						
AMNH 20006	<i>A. pangan</i>									49.5*	27.0
AMNH 20011 (right)	<i>A. crassum</i>	16.7	7.2	16.5	9.2	16.8*	12.2	20.5	15.4	31.9	17.3
AMNH 20011 (left)	<i>A. crassum</i>									32.4	17.3
AMNH 20015 (right)	<i>A. birmanicum</i>									29.0*	14.9
AMNH 20015 (left)	<i>A. birmanicum</i>									28.4	15.0
AMNH 20017 (right)	<i>A. tenuis</i>	10.5*	4.9	10.2*	5.5	8.4	6.1	11.4*	7.7	20.0	9.0
AMNH 20017 (left)	<i>A. tenuis</i>	10.6	4.8	10.0	5.5	8.6	6.0	11.4	7.6	19.7	9.3
AMNH 20028	<i>A. crassum</i>	18.6	8.2	17.2	9.8						
AMNH 20029	<i>A. crassum</i>									37.9	19.9
AMNH 32522	<i>A. crassum</i>					18.7	13.2	23.5*	15.5*		
GSI B605	<i>A. birmanicum</i>	[14.9]	[5.8]	14.3	7.7	14.0	9.5	18.0	13.4	29.7	16.0
GSI B607	<i>A. pangan</i>									52.7	29.7
GSI B612	<i>A. crassum</i>				[10.8]	[16.7]	[11.8]	[23.7]	[17.4]		
GSI B613	<i>A. crassum</i>									38.2	20.5
GSI B614	<i>A. crassum</i>	21.3	9.8								
GSI B617	<i>A. pangan</i>			19.3	12.4	19.5*	16.5*	26.1	21.9	36.7	22.2
GSI B620	<i>A. pangan</i>									47.7	24.5
GSI B626	<i>A. tenuis</i>					9.2	6.0				
GSI B627	<i>A. tenuis</i>							11.7	7.4	18.0	8.7
GSI B745	<i>A. pangan</i>	24.1	12.7	21.7	14.1	21.5*	15.0*	30.8	21.9		
GSI B751	<i>A. crassum</i>	19.8	9.9	19.7	11.3	16.8	12.9	23.9	18.8	39.2	21.8
GSI B755	<i>A. tenuis</i>	[11.7]	[4.3]	11.3	5.6	9.3	6.4	11.6	8.1	21.0	9.4
GSI B760	<i>A. tenuis</i>					[9.1]	[5.2]				
GSI B761	<i>A. tenuis</i>	11.9	3.9								
GSI B767	<i>A. birmanicum</i>			12.9	7.0	12.9	9.9	15.5	11.8		



## SHORT NOTES

# Permian orthoconic cephalopods of the Ochiai Formation in the Southern Kitakami Mountains, Northeast Japan

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## Introduction and geologic setting

Middle to Upper Permian strata in the Southern Kitakami Mountains, Northeast Japan, contain a relatively diverse orthoconic cephalopod assemblage. Although they were the subject of investigations by Hayasaka (1924), Shimizu and Obata (1936), Ouchi (1971) and Koizumi (1975), information from the Southern Kitakami Mountains has been ignored in modern cephalopod taxonomy owing to a lack of adequate illustrations and descriptions. Knowledge of Middle to Late Permian orthoconic cephalopods is very limited and comes mainly from the Peri-Gondwana region that includes Iran (e.g., Teichert and Kummel, 1973), Oman (Niko *et al.*, 1996), the Salt Range (Waagen, 1879), Timor (Haniel, 1915), and the South China region (e.g., Zhao *et al.*, 1978). Revision of the Kitakami fauna, therefore, may be of phylogenetic and paleobiogeographic importance. In view of this, the present study focuses on orthocerid species from the Kamiyasse area, Miyagi Prefecture, and an adjoining area to the north in Iwate Prefecture (Figure 1). The repository for these specimens is the University Museum of the University of Tokyo (UMUT).

In an earlier geologic study, Tazawa (1973) investigated the Kamiyasse area, and elucidated the detailed lithostratigraphy of the Permian deposits as the Sakamotozawa, Kanokura and Toyoma series. With the exception of the lowest, carbonate-rich strata assigned to the Nakadaira Formation, most of these series were synthesized and assigned in the subsequent works of Ehiro (1974, 1977) to the Ochiai Formation (Onuki, 1969), from which the present cephalopod specimens were collected. The Ochiai Formation is divisible into three members: the Toyazawa

Member (Ehiro, 1977), consisting of sandstone interbedded with calcareous shale and impure limestone layers, represents the middle part of the formation, whereas the unnamed lower and upper members are mainly massive shale with minor amounts of conglomerate, sandstone and limestone.

## Systematic paleontology

Order Orthocerida Kuhn, 1940  
Superfamily Orthoceratoidea M'Coy, 1844  
Family Brachycycloceratidae Furnish, Glenister  
and Hansman, 1962  
Genus *Brachycycloceras* Miller,  
Dunbar and Condra, 1933

*Type species.* — *Brachycycloceras normale* Miller,  
Dunbar and Condra, 1933.

## *Brachycycloceras* sp.

Figure 2.1, 2.2

*Description.*—Single, deformed orthocone, 56 mm in length, consisting of annulated, apical phragmocone with gently curved (exogastric?) apical shell; shell expansion rapid for orthoceratids. Prominent annulations form rounded to bluntly pointed crests and deep interspaces that appear as rounded concavities in longitudinal profile; annulations quite oblique, slope toward dorsal (?) side. Except for weak dorsal (?) sinus, sutures run roughly parallel to annulations.

*Discussion.*—No siphuncular structure is preserved in this specimen. However, its rapidly expanded shell with



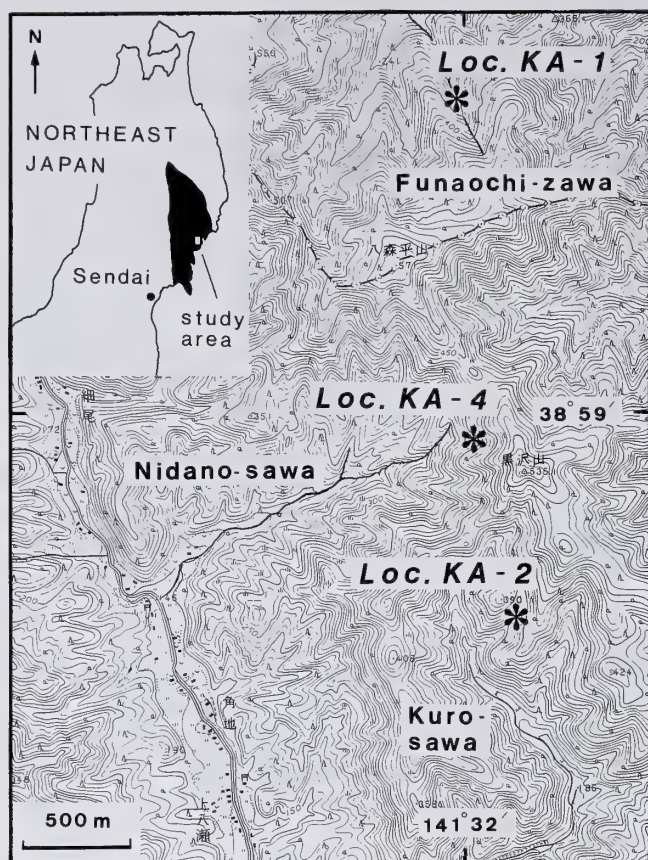


Figure 1. Index map of fossil localities in the Southern Kitakami Mountains (inset), using the 1:25,000 map of "Shishiori" published by the Geographical Survey Institution.

gently curved apical part and strongly prominent annulations warrant generic assignment to *Brachycycloceras*. In addition to *Brachycycloceras* sp. from the Early Permian of western Australia (Teichert, 1951) and *B. rustaqense* Niko, Pillevuit and Nishida, 1996, from the Wordian (Middle Permian in a three-fold division) of the central Oman Mountains, this discovery represents the third Permian occurrence of the genus.

**Material examined and occurrence.**—UMUT PM 28065. This specimen was recovered as float from shale in the Funaochi-zawa Valley at locality KA-1 (Figure 1). Judging from the lithofacies of the matrix, the geology around this locality, and the associated ammonoid fauna, it was probably derived from the middle-upper portion (Roadian–Wordian; Middle Permian) of the lower member of the Ochiai Formation.

Family Geisonoceratidae Zhuravleva, 1959  
cf. Geisonoceratid, genus and species uncertain

Figure 2.4, 2.7

**Discussion.**—A deformed body chamber of an orthoconic shell, 115 mm in length, is available for this study. This specimen is tentatively considered to be a geisonoceratid, because of the characteristic ornamentation of its transverse ridges that indicates asymmetrical (steep side towards aperture) longitudinal profiles, and because of the absence of a shell constriction. Similar ornamentation is also known to occur in some Carboniferous bactritoids, such as *Ctenobactrites isogramma* (Meek, 1871; Sturgeon *et al.*, 1997, pl. 1-1, figs. 8–11, pl. 1-42, fig. 3) and *Bactrites peytonensis* Mapes (1979, pl. 8, figs. 7, 11), although characteristic dorsal carina and/or well-developed wrinkle-layer of ornamented bactritoids are not recognized in this specimen.

**Material examined and occurrence.**—UMUT PM 28066. This specimen was recovered as float in talus deposits of shale located on a tributary of the Kuro-sawa Valley (locality KA-2), where the upper member is exclusively distributed. Based on ammonoids collected near this locality, Ehro and Araki (1997) inferred a late Capitanian (Middle Permian) age for the cephalopod-bearing shale of the lower part of the upper member of the Ochiai Formation.

Superfamily Pseudorthoceratoidea Flower  
and Caster, 1935

Family Pseudorthoceratidae Flower and Caster, 1935

Subfamily Spyroceratinae Shimizu and Obata, 1935

Genus *Lopingoceras* Shimanskiy in Ruzhentsev, 1962

**Type species.**—*Orthoceras lopingense* Stoyanow, 1909.

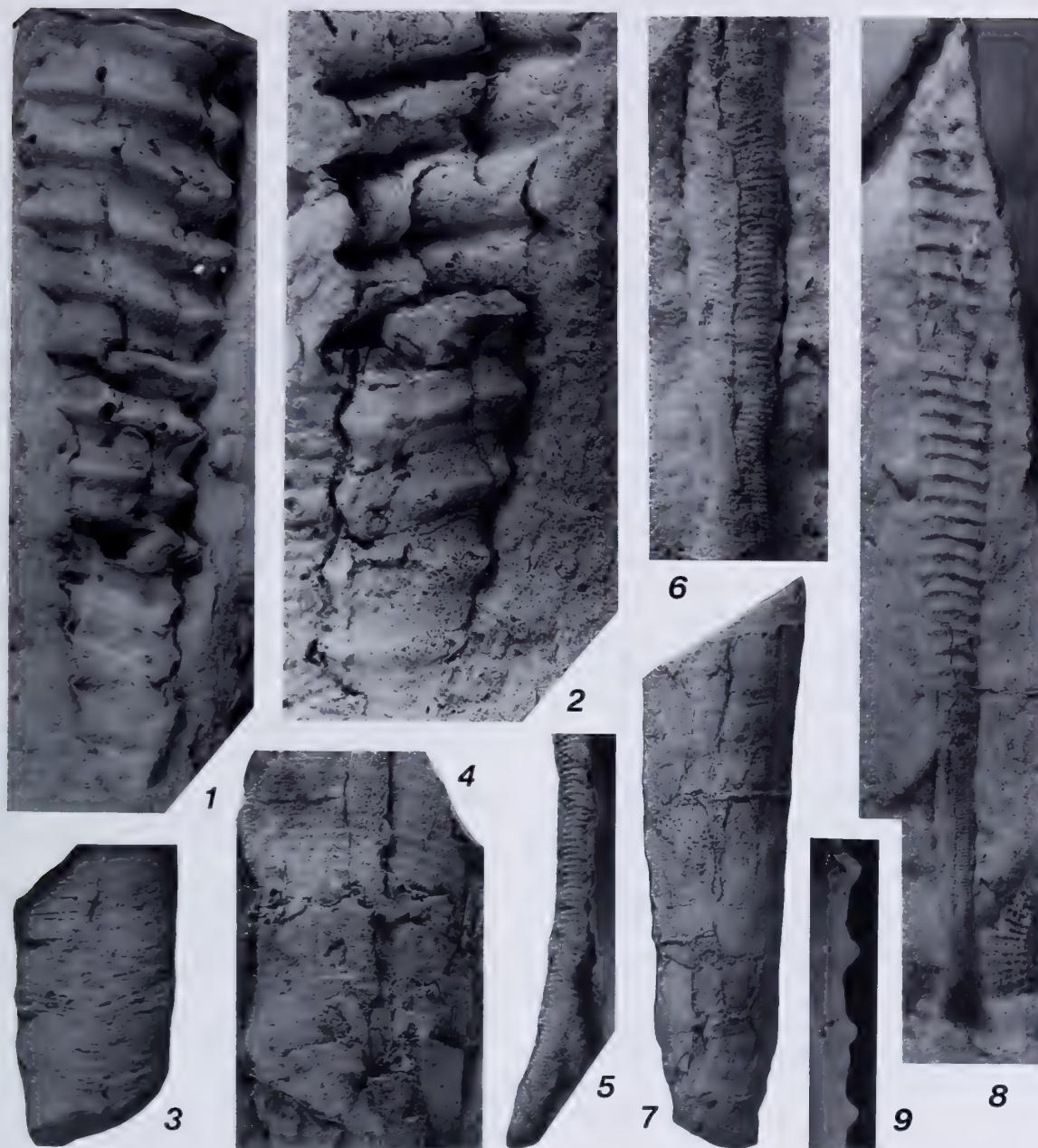
**Other included species.**—*Lopingoceras acutanolatum* Zhao, Liang and Zheng, 1978; *L. cf. acutanolatum* (this report); *L. bicinctum* (Abich, 1878); *L. cyclophorum* (Waagen, 1879); *L. guangdeense* Zhao, Liang and Zheng, 1978; *L. hayasakai* Niko and Ozawa, 1997; *L. margaritatum* (Abich, 1878); *L. maubesiense* (Haniel, 1915); *L. ? obliqueannulatum* (Waagen, 1879); *L. sp.* (Teichert *et al.*, 1973), and *L. sp.* (Zheng, 1984).

**Range.**—Known from the late Gzhelian (Late Carboniferous)–early Asselian (Early Permian) boundary through the Changhsingian (Late Permian).

**Diagnosis.**—Early juvenile shell gently curved, nonannulated with transverse surface lirae. See Shimanskiy in Ruzhentsev (1962, p. 90) for diagnosis of adult shell, which we accept.

**Discussion.**—The distinction between *Lopingoceras* and the Early Carboniferous genus *Cycloceras* (M'Coy, 1844; type and only reliably included species, *Orthoceras laevigatum* M'Coy, 1844, see Histon, 1991, and BZN 50, 1993, opinion 1720) has long been plagued by an inadequate description of the latter's type species. Except for differences in age range, the former differs from the latter only in the shape of annulations, i.e., *Cycloceras* having





**Figure 2.** 1, 2. *Brachycycloceras* sp., UMUT PM 23065. 1, lateral view of silicone rubber cast, venter on left (?),  $\times 2$ ; 2, external mold with steinkern of apical shell, note gently curved shell and sutures, venter on right (?),  $\times 3$ . 3. Orthoceras, superfamily, family, genus and species uncertain, UMUT PM 28068, side view,  $\times 2$ . 4, 7. Cf. geisonoceratid, genus and species uncertain, UMUT PM 28066. 4, details of surface ornamentation, silicone rubber cast,  $\times 2$ ; 7, steinkern, side view,  $\times 1$ . 5, 6, 8, 9. *Lopingoceras* cf. *acutanolatum* Zhao, Liang and Zheng, 1978, UMUT PM 28067, silicone rubber cast. 5, details of early juvenile shell,  $\times 4$ ; 6, details of ornamentation of nonannulated part,  $\times 5$ ; 8, side view,  $\times 2$ ; 9, details of annulations, note triangular longitudinal profiles,  $\times 5$ .

contiguous annulations with equally rounded crests and interspaces, whereas in *Lopingoceras* the annulations are more or less distant in spacing and have triangular profiles. Whether these external differences are of supraspecific

rank seems questionable in modern taxonomy. The Kitakami material described herein includes the first known example of an early juvenile shell of *Lopingoceras*, whose characters add to the generic concept. The taxonomic

problem will be solved when the apical shell morphology and internal structure of *Cycloceras laevigatum* are known well enough for comparison with the newly refined diagnosis of *Lopingoceras*.

*Lopingoceras* cf. *acutanolatum* Zhao,  
Liang and Zheng, 1978

Figure 2.5, 2.6, 2.8, 2.9

Compare with.—

*Lopingoceras acutanolatum* Zhao, Liang and Zheng, 1978, p. 63,  
64, pl. 31, figs. 11, 12, pl. 33, figs. 3, 4.

**Description.**—This species represented by a single external mold of gradually expanded shell, 65 mm in length, whose adoral part is strongly deformed, with no internal structure preserved; adoral end attains approximately 4 mm (reconstructed as circular cross section) in shell diameter. Nonannulated early juvenile shell gently curved, with circular cross section and transverse lirae; this nonannulated part, approximately 21.5 mm in length, followed by monotonously annulated shell where lirae disappear; embryonic shell may be cone-shaped; annulations may be roughly transverse with wide spacing for genus, with triangular longitudinal profiles and pointed crests; there are 1–2 annulations in corresponding reconstructed shell diameter; interspaces probably weakly depressed.

**Discussion.**—The annulation shape and spacing of the present specimen strongly resemble *Lopingoceras acutanolatum* from the Wuchiapingian (Late Permian) Laoshan Shale in South China. Nevertheless, since *L. acutanolatum* is described from fragmentary specimens and its apical shell morphology is unknown, the Kitakami specimen is only provisionally assigned to this species. Comparison between *Lopingoceras* cf. *acutanolatum* and figured specimens from the Ochiai Formation cited as *Lopingoceras* ? sp. by Koizumi (1975) is impossible. Judging from his illustrations (Koizumi, 1975, pl. 4, figs. 4, 5), the specimens are inadequate for systematic treatment because of poor preservation.

**Material examined and occurrence.**—UMUT PM 28067. This specimen was collected from a float block of shale in the riverbed of the Nidano-sawa Valley at locality KA-4. The exact stratigraphic horizon from which this block was derived is unknown, but it is highly likely that this block came from the middle part of the Toyazawa Member of the Ochiai Formation, based on its lithofacies and collected locality. Thus, this specimen is considered to be of Wordian (or Capitanian) age.

Superfamily, family, genus and species uncertain

Figure 2.3

**Discussion.**—A fragmentary specimen of a deformed orthoconic shell, 22 mm in length, shows transverse lirae that consist of alternating strongly prominent and less prominent ridges. Similar ornamentation occurs in several post-Carboniferous orthocerid genera; such as the orthoceratid *Trematoceras* (Eichwald, 1851), the geisonoceratid *Pseudotemperoceras* (Stschastlivtseva, 1986), and the pseudorthoceratid *Dolorthoceras* (Miller, 1931). No internal structures are preserved in the present specimen, so it cannot be identified even to the superfamily level.

**Material examined and occurrence.**—UMUT PM 28068. Same as the specimen above assigned to cf. geisonoceratid, genus and species uncertain.

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# INDEX OF GENERA AND SPECIES (vol. 5, no. 1–vol. 6, no. 4: 2001–2002 )

Genera and species described in volumes 5–6 of Paleontological Research are listed in alphabetical order. The volume number, part number (in parentheses), page numbers, and figure numbers are given for each taxon. Newly proposed taxa are in bold type.

## A

- vol. (no.), page, fig (s)
- Abadehella* sp. ....6(4), ? fig. 9
- Acanthocythereis dunelmensis* .....6(1), 10, fig. 7
- Acanthocythereis fujinaensis* .....6(1), 5, figs. 5, 7
- Acanthocythereis izumoensis* .....6(1), 5, figs. 5, 8
- Acanthocythereis koreana* .....6(1), 10, fig. 7
- Acanthocythereis tsurugasakensis* .....6(1), 14, fig. 8
- "*Acanthotriletes*" *menendezii* .....6(1), 27, fig. 3
- Acila* (*Acila*) *kiiensis* .....6(3), 261, fig. 3
- Acila* (*Truncacila*) cf. *nagaoi* .....6(2), 136, fig. 5
- Agathammina* cf. *pusilla* .....6(4), ? fig. 9
- Agathammina*? sp. ....6(4), ? fig. 9
- Agathiceras uralicum* .....5(3), 207, fig. 6
- Alispiriferella japonica*** .....5(4), 300, fig. 8
- Alispiriferella ordinaria* .....5(4), 300, fig. 8
- Almerarhynchia* .....5(4), 326
- Almerarhynchia pocoviana* .....5(4), 328, fig. 5
- Alveolophragmium* sp. ....6(2), 162, fig. 9
- Ambtonia obai* .....6(1), 88, fig. 3
- Ambtonia shimanensis* .....6(1), 5, fig. 5
- Ambtonia takayasui* .....6(1), 5, fig. 5
- Ammobaculites* sp. ....6(2), 162, fig. 9
- Ammodiscus* sp. ....6(2), 158, fig. 7
- Amphileberis nipponica* .....6(1), 90, fig. 5
- Ancistrolepis fragilis* var. ....5(3), 220, fig. 3
- Anemonaria sublaevis* .....6(3), 290, fig. 4
- Angulogerina hannai* .....6(2), 164, fig. 10
- Angulus maximus* .....6(1), 108, figs. 7, 9
- Anodonta woodiana* .....5(1), 34, figs. 1–2
- Anthracohyus choeroides* .....6(4), ? fig. 10
- Anthracotherium* .....6(4), ? figs. 3–6
- Arca* (*Arca*) *uedai*** .....6(2), 136, fig. 5
- Artioceras rhipaeum* .....5(3), 204, fig. 3
- Auria munechikai* .....6(1), 90, fig. 5
- Aurila* sp. ....5(4), 247, fig. 5
- Aurila spinifera* .....6(1), 88, fig. 3
- Australimoosella tomokoae* .....6(1), 90, fig. 5

## B

- Bactrites nagatoensis* .....5(2), 117, fig. 2
- Bactrites* sp. ....5(2), 117, fig. 2
- Bairdia beraguensis* .....6(2), 198, fig. 2
- Bandicota bengalensis* .....6(3), 249, fig. 11

- Bandicota* sp. cf. *B. bengalensis* ....6(3), 247, figs. 9, 10
- Barbatia mytiloides* .....5(1), 70, fig. 9
- Bathysiphon eocenica* .....6(2), 158, fig. 7
- Bathysiphon vernoni* .....6(2), 158, fig. 7
- Belbekella* .....5(4), 326
- Belbekella mutabilis* .....5(4), 325, fig. 4
- Blaspirifer* cf. *reedi* .....5(4), 300, fig. 8
- Bogoslovskya omiensis*** .....5(2), 116, fig. 1
- Botula hortensis* .....5(1), 59, fig. 1
- Brachycycloceras* sp. ....6(4), ? fig. 2
- Brazilea scissa* .....6(1), 34, fig. 7
- Brevitriletes levis* .....6(1), 27, fig. 3
- Bseptatoechia inflata* .....5(4), 325, fig. 4
- Buccinum aomoriensis* .....5(3), 220, fig. 3
- Buccinum bulimiloideum* .....5(3), 218, fig. 2
- Buccinum inclytum* .....5(3), 220, fig. 3
- Buccinum middendorffi* .....5(3), 218, figs. 2, 3
- Buccinum ochotense* .....5(3), 218, fig. 2
- Buccinum rhodium* .....5(3), 220, fig. 3
- Buccinum saitoi*** .....5(3), 218, fig. 2
- Buccinum shibatense*** .....5(3), 218, fig. 2
- Buccinum sinanoense* .....5(3), 220, fig. 3
- Buccinum striatissimum* .....5(3), 218, fig. 2
- Buccinum tsubai* .....5(3), 218, fig. 2
- Buccinum unuscarinatum* .....5(3), 220, fig. 3
- Budashevaella* sp. aff. *B. multicamerata* ..6(2), 158, fig. 7
- Budashevaella symmetrica* .....6(2), 158, fig. 7
- Buettneria howardensis* .....6(1), 55, fig. 13
- Buettneria maleriensis* .....6(1), 43, figs. 1–16
- Bulimina schwageri* .....6(2), 164, fig. 10
- Burrirhynchia* .....5(4), 326
- Burrirhynchia leightonensis* .....5(4), 322, figs. 2, 5

## C

- Calamospora* sp. cf. *C. sinuosa* .....6(1), 27, fig. 3
- Callistocythere alata* .....6(1), 88, fig. 3
- Callistocythere asiatica* .....6(1), 88, fig. 3
- Callistocythere hatatensis* .....5(4), 247, fig. 5
- Callistocythere hayamensis* .....6(1), 88, fig. 3
- Callistocythere japonica* .....6(1), 6, fig. 6
- Callistocythere kotorai* .....5(4), 247, fig. 5
- Callistocythere kyongjuensis* .....6(1), 6, fig. 6
- Callistocythere* sp. ....5(4), 247, fig. 5
- Callistocythere* sp. ....6(1), 88, fig. 3



- Callistocythere undata* .....6(1), 88, fig. 3  
*Calyptrea sp.* .....6(2), 136, fig. 5  
*Cameleolopha (Hyotissocameleo) tissoti* .....  
 .....5(2), 78, figs. 2, 3, 5, 7  
*Campages sp.* .....5(2), 90, fig. 3  
*Cancrinella cf. spinosa* .....5(4), 290, fig. 6  
*Cancrinella? cancrini* .....6(3), 290, fig. 4  
*Cannanoropollis densus* .....6(1), 34, fig. 7  
*Cannanoropollis korbaensis* .....6(1), 32, fig. 6  
*Capillomesolobus sp.* .....5(4), 290, fig. 6  
*Carthaginites* .....6(4), ?  
*Carthaginites asiaticus* .....6(4), ? fig. 1  
***Carthaginites yamashitai*** .....6(4), ? figs. 2-3  
*Carwinula sp.* .....6(1), 90, fig. 5  
*Cetotheriidae gen. et sp. indet.* .....6(2), 180, figs. 1, 2, 5  
*Chasmagnathus convexus* .....5(4), 264, fig. 2  
*Chilostomella ovoidea* .....5(3), 194, fig. 1  
*Chlamys (Leochlamys) namigataensis* .....  
 .....6(2), 136, figs. 5, 6  
*Chlamys acroporicola* .....5(1), 65, fig. 5  
*Chlamys sp.* .....6(1), 107, figs. 6, 7  
*Cibicides elamaensis* .....6(2), 155, fig. 11  
*Cibicides sp.* .....6(2), 155, fig. 11  
*Cibicoides pseudoungerianus* .....5(3), 194, fig. 1  
*Cibolaites molenaari* .....5(1), 46, fig. 1  
*Cinnalepeta pulchella* .....5(1), 27, fig. 6  
*Cirbroelphidium wakkanabense* .....6(2), 168, fig. 12  
*Cistecephaloides boonstrai* .....5(3), 187, fig. 11  
*Cistecephalus microrhinus* .....5(3), 179, figs. 2, 8-11  
*"Clavulina" sp.* .....6(2), 162, fig. 9  
*Cletocythereis sp.* .....6(1), 88, fig. 3  
*Cluthia subjaponica* .....6(1), 5, figs. 5, 6  
*Cluthia tamayuensis* .....6(1), 5, figs. 5, 6  
*Colaniella parva* .....6(4), ?, fig. 8  
*Collignoniceras praecox* .....5(1), 46, fig. 1  
*Collignoniceras woollgari regulare* .....5(1), 46, fig. 1  
*Collignoniceras woollgari woollgari* .....5(1), 46, fig. 1  
*Compressopproductus corniformis* .....6(3), 290, fig. 4  
*Comucoquimba moniwensis* .....5(4), 247, fig. 5  
*Comucoquimba saitoi* .....5(4), 247, fig. 5  
*Conquimba spp.* .....5(4), 247, fig. 5  
*Coptothyris grayi* .....5(2), 90, figs. 3, 8, 9  
*Coquimba cf. ishizakii* .....5(4), 247, fig. 5  
*Coquimba sp.* .....5(4), 247, fig. 5  
*Cornucoquimba moniwensis* .....5(4), 247, fig. 5  
*Cornucoquimba saitoi* .....5(4), 247, fig. 5  
*Cornucoquimba tosaensis* .....6(1), 90, fig. 5  
*Costabuntonia hartmanni* .....6(2), 200, fig. 3  
*Costatascyclus crenatus* .....6(1), 32, fig. 6  
*Crassatella yabei* .....6(1), 108, fig. 7, 9  
*Crassostrea sp.* .....6(2), 138, fig. 6  
*Cravenoceras incisum* .....5(3), 205, fig. 4  
*Crenatula nakayamai* .....5(1), 63, fig. 4  
*Cretirhynchia bohémica* .....5(4), 325, fig. 4  
*Cretirhynchia* .....5(4), 323  
*Cretirhynchia aff. cuneiformis* .....5(4), 324, fig. 3  
*Cretirhynchia bohémica* .....5(4), 325, fig. 4  
*Cretirhynchia exsculpta* .....5(4), 324, fig. 3  
*Cretirhynchia minor* .....5(4), 324, fig. 3  
*Cretirhynchia plicatilis* .....5(4), 322, fig. 2  
*Cretirhynchia sp.* .....5(4), 324, fig. 3  
*Cretirhynchia sp.* .....5(4), 324, fig. 3  
*Cribroelphidium ishikariense* .....6(2), 155, fig. 11  
*Cribroelphidium sorachiense* .....6(2), 155, fig. 11  
*Cribroelphidium sp.* .....6(2), 168, fig. 12  
*Cribrostomoides sp. cf. C. cretacea* .....6(2), 158, fig. 7  
*Crimites subkrotowi* .....5(3), 207, fig. 6  
*Cristatisporites inconstans* .....6(1), 30, fig. 5  
*Cryptoseptida sp.* .....6(4), ?, fig. 9  
*Cultellus izumoensis* .....6(1), 108, figs. 7, 9  
*Curvemysella paula* .....5(1), 67, fig. 7  
*Cushmanidea bhatiai* .....6(2), 200, fig. 3  
*Cyclammia ezoensis* .....6(2), 162, fig. 9  
*Cyclammia pacifica* .....6(2), 162, fig. 9  
*Cyclammia sp.* .....6(2), 162, fig. 9  
*Cyclammia sp. aff. C. pusilla* .....6(2), 162, fig. 9  
*Cyclocardia sp.* .....6(2), 138, fig. 6  
*Cyclogranisporites minutus* .....6(1), 27, fig. 3  
*Cyclograpsus intermedius* .....5(4), 263, figs. 1, 2  
*Cyclothyris* .....5(4), 323  
*Cyclothyris aff. difformis* .....5(4), 321, fig. 1  
*Cyclothyris antidichotoma* .....5(4), 322, fig. 2  
*Cyclothyris difformis* .....5(4), 321, fig. 1  
*Cyclothyris antidichotoma* .....5(4), 322, fig. 2  
*Cythere omotenipponica* .....5(4), 247, fig. 5  
*Cytherella mohani* .....6(2), 198, fig. 2  
*Cytherella sp.* .....6(2), 198, fig. 2  
*Cytherelloidea bhatiai* .....6(2), 198, fig. 2  
*Cytheromorpha acupunctata* .....6(1), 88, fig. 3  
***Cytheromorpha godavariensis*** .....6(2), 198, fig. 2  
*Cytheropteron cf. sawanense* .....5(4), 247, fig. 5  
***Cytheropteron kumaii*** .....6(1), 94, fig. 8  
*Cytheropteron miurense* .....5(4), 247, fig. 5  
*Cytheropteron subuchioi* .....5(4), 247, fig. 5  
*Cytherura duddukuruensis sp. nov.* .....6(2), 202, fig. 4  
*Cytherura miii* .....6(1), 90, fig. 5

## D

- Daraelites elegans* .....5(3), 204, fig. 3  
*Darwinula sp.* .....6(1), 94, fig. 8  
*Delectopecten sp.* .....6(2), 136, fig. 5  
*Dendropoma* .....5(1), 5, fig. 2  
*Dendropoma annulatum* .....5(1), 4, fig. 1  
*Dendropoma sp.* .....5(1), 4, figs. 1, 3-6  
*Dentalina sp. cf. D. subsoluta* .....6(2), 164, fig. 10

- Derbyia* sp. ....5(4), 294, fig. 7  
*Dielasma* sp. ....5(4), 300, fig. 8  
*Diplosphaera* ....5(2), 138  
*Diplosphaera hexagonalis* ....5(2), 133, fig. 2  
*Durrirhynchia leightonensis* ....5(4), 322, fig. 2  
*Dzhulfoceras* cf. *furnishi* ....5(2), 113, fig. 2  
*Dzhulfoceras* sp. ....5(2), 113, fig. 2

## E

- Echigoceras* ....6(4), ?  
*Echigoceras sasakii* ....6(4), ?, figs. 1–4  
*Echinauris* sp. ....6(3), 290, fig. 4  
*Ecnomiosa* sp. ....5(2), 90, fig. 3  
*Elphidium advenum* ....5(3), 194, fig. 1  
*Emydops minor* ....5(3), 184, fig. 7  
*Emydops platyceps* ....5(3), 179, figs. 2, 5–7  
*Enteles* sp. ....5(4), 294, fig. 7  
*Entolium inequivalve* ....5(2), 125, fig. 4  
*Eolasiolus* sp. ....6(4), ?, fig. 8  
*Epicanites loeblichii* ....5(3), 205, fig. 4  
*Eucytherura neolae* ....5(4), 247, fig. 5  
*Evolutinella subamakusaensis* ....6(2), 160, fig. 8

## F

- Fallaxoproductus moribuensis* ....5(4), 294, fig. 7  
*Falsobuntonia hayamii* ....6(1), 88, figs. 3, 5  
*Falsocythere elongata* ....6(2), 202, fig. 4  
*Finmarchinella japonica* ....5(4), 247, fig. 5  
*Fissurina* sp. cf. *F. marginata* ....6(2), 164, fig. 10  
*Florinites occultus* ....6(1), 32, fig. 6  
*Florinites* sp. ....6(1), 30, fig. 5  
*Frenulina* ....5(2), 92, fig. 5  
*Frenulina sanguinolenta* ....5(2), 90, figs. 3, 8, 9  
*Frieleia halli* ....6(3), 317, fig. 13  
*Fursenkoina pauciloculata* ....5(3), 196, fig. 2

## G

- Galeomma* cf. *polita* ....5(1), 66, fig. 6  
*Girtyoceras meslerianum* ....5(3), 205, fig. 4  
*Glandulina laevigata ovata* ....6(2), 164, fig. 10  
*Globobulimina* sp. ....6(2), 164, fig. 10  
*Globocassidulina globosa* ....6(2), 164, fig. 10  
*Globotruncana arca* ....5(4), 280, fig. 4  
*Globotruncana arca* ....5(4), 280, fig. 4  
*Globotruncana linneiana* ....5(4), 280, fig. 4  
*Glomospira* sp. ....6(2), 158, fig. 7  
*Glycymeris (Glycymeris) sp.* ....6(2), 136, fig. 5  
*Glycymeris cisshuensis* ....6(1), 108, fig. 7  
*Golunda kelleri* ....6(3), 250, fig. 12  
*Golunda tatroticus* ....6(3), 250, figs. 12–15

- Goniomya* sp. ....5(2), 125, fig. 4  
*Granulatisporites austroamericanus* ....6(1), 27, figs. 3, 4  
*Grapsus albolineatus* ....5(4), 264, figs. 1, 2  
*Grapsus tenuicrustatus* ....5(4), 264, fig. 2  
*Grasirhynchia* ....5(4), 326  
*Grasirhynchia grasiana* ....5(4), 328, fig. 5  
*Grtapsus albolineatus* ....5(4), 263, fig. 1  
*Guttulina takyanagii* ....6(2), 164, fig. 10  
*Gypospirifer volatilis* ....5(4), 300, fig. 8

## H

- Hanaiborchella triangularis* ....5(4), 247, fig. 5  
*Haplophragmoides crassiformis* ....6(2), 160, fig. 8  
*Haplophragmoides rugosus soyaensis* ....6(2), 160, fig. 8  
*Haplophragmoides tanaii* ....6(2), 160, fig. 8  
*Haplophragmoides yokoyamai* ....6(2), 160, fig. 8  
*Haplophragmoides* spp. ....6(2), 160, fig. 8  
*Hapsicytheridea undulata* ....6(2), 202, fig. 4  
*Haraiborchella triangularis* ....5(4), 247, fig. 5  
*Helice leachi* ....5(4), 264, figs. 1, 2  
*Hemicythere kitanipponica* ....5(4), 249, fig. 6  
*Hemicytherura cuneata* ....5(4), 249, fig. 6  
*Hemicytherura* spp. ....6(1), 90, fig. 5  
*Hemigrapsus sanguinensis* ....5(4), 264, figs. 1, 2  
*Hermanites posterocostatus* ....5(4), 249, fig. 6  
*Hermanites sastryi* ....6(2), 202, fig. 4  
*Heterolepa poronaiensis* ....6(2), 155, fig. 11  
*Heterolepa subhaidingeri* ....5(3), 194, fig. 1  
*Holcopocythere bassiporosa* ....6(2), 200, fig. 3  
*Hornibrookella tewarii* ....6(2), 202, fig. 4  
*Horriditriteles* ....6(1), 31  
*Horriditriteles ramosus* ....6(1), 27, fig. 3  
*Horriditriteles ramosus* ....6(1), 28, fig. 4  
*Horriditriteles uruguayensis* ....6(1), 27, fig. 3  
*Horriditriteles uruguayensis* ....6(1), 28, fig. 4  
*Hourcquia hataii* ....5(2), 105, figs. 6–8  
*Hourcquia ingens* ....5(2), 103, figs. 2–5  
*Hourcquia kawashitai* ....5(2), 107, figs. 9–12  
*Hustedia ratburiensis* ....5(4), 300, fig. 8  
*Hytissocameleo* ....5(2), 83  
*Hypoturrilites* ....5(4), 229  
*Hypoturrilites gravesianus* ....5(4), 230, fig. 1  
*Hypoturrilites komotai* ....5(4), 232, fig. 3  
*Hypoturrilites nodiferus* ....5(4), 236, figs. 6–7  
*Hypoturrilites wrighti* ....5(4), 230, figs. 1–2  
*Hypoturrilites yabei* ....5(4), 235, fig. 5

## I

- Illinites unicus* ....6(1), 34, fig. 7  
*Inoceramus teshioensis* ....5(2), 105, fig. 6  
*Ishizakiella miurensis* ....6(1), 88, figs. 3, 5



- Isognomon (Hippochaeta) hataii* .....6(2), 136, figs. 5, 6  
*Isognomon (Hippochaeta) maxillatus* .....5(1), 70, fig. 9  
*Ityophorus undulatus* .....6(1), 76, figs. 3, 4

## J

- Jolonica nipponica* .....5(2), 90, figs. 3, 8, 9  
*Juresania cf. juresanensis* .....5(4), 290, fig. 6

## K

- Kamurana? sp.* .....6(4), ?, fig. 9  
*Kaninospirifer sp.* .....6(3), 290, fig. 4  
*Kawingasaurus fossilis* .....5(3), 187, fig. 11  
*Kixicibca bizijuebsus* .....5(4), 248, fig. 6  
*Kobayashiina donghaiensis* .....6(1), 90, fig. 5  
*Kotoracythere abnorma* .....5(4), 249, fig. 6  
*Kotoracythere tsukagoshii* .....6(1), 5, figs. 5, 6  
*Krasnoyarichthys* .....6(3), 322  
*Krasnoyarichthys jesseni* .....6(3), 323, fig. 2  
*Krithe bhandarii* .....6(2), 200, fig. 3  
*Krithe japonica* .....6(1), 90, fig. 5

## L

- Laevigatosporites vulgaris* .....6(1), 30, fig. 5  
*Lagena striata* .....6(2), 164, fig. 10  
*Lahirites segmentatus* .....6(1), 35, figs. 8, 9  
*Lamellaerhynchia geokderensis* .....5(4), 328, fig. 5  
*Lamellaerhynchia* .....5(4), 326  
*Laperousecythere ikeyai* .....6(1), 5, figs. 5, 7  
*Laqueus blanfordi* .....5(2), 97, fig. 9  
*Laqueus rubellus* .....5(2), 90, fig. 3  
*Laqueus sp.* .....5(2), 96, figs. 8, 9  
*Leiotriletes sp.* .....6(1), 27, fig. 3  
*Lenticulina sp.* .....6(2), 164, fig. 10  
*Leptodus nobilis* .....5(4), 294, fig. 7  
*Limatula iwayae* .....5(2), 125, fig. 4  
*Lingula anatina* .....5(1), 67, figs. 7, 8  
*Linoproductus lineatus* .....5(4), 290, fig. 6  
*Lithophaga sp.* .....5(1), 65, fig. 5  
*Lopingoceras cf. acutanolatum* .....6(4), ? fig. 2  
*Loxoconcha japonica* .....6(3), 266, figs. 1, 3, 5, 7, 9  
*Loxoconcha liljeborgii* .....6(3), 269, figs. 3, 5, 7, 9  
*Loxoconcha nozokiensis* .....5(4), 249, fig. 6  
*Loxoconcha optima* .....6(1), 88, figs. 3, 5  
*Loxoconcha optima* .....6(3), 266, fig. 1  
*Loxoconcha ozawai* .....6(3), 266, fig. 1  
*Loxoconcha pulchra* .....6(1), 88, figs. 3, 5  
*Loxoconcha pulchra* .....6(3), 266, fig. 1  
*Loxoconcha shanhaiensis* .....6(3), 270, figs. 4-7, 9  
*Loxoconcha spp.* .....6(1), 90, fig. 5  
*Loxoconcha tosaensis* .....6(1), 88, figs. 3, 5

- Loxoconcha tumulosa* .....6(3), 270, figs. 4, 5, 9  
*Loxoconcha uranouchiensis* .....6(1), 90, fig. 5  
*Loxoconcha uranouchiensis* .....6(3), 266, fig. 1  
*Loxoconcha viva* .....6(1), 88, figs. 3, 5  
*Loxocorniculum sp.* .....5(4), 249, fig. 6  
*Lunucammina cf. palmata* .....6(4), ?, fig. 8

## M

- Mactra? sp.* .....6(2), 138, fig. 6  
*Maja* .....6(2), 213  
*Maja tomidai* .....6(2), 214, figs. 3, 4, 5  
*Malleus anatinus (Gmelin)* .....5(1), 60, fig. 2  
*Malleus malleus (Linnaeus)* .....5(1), 60, fig. 2  
*Mantellicera japonicum* .....5(4), 234, fig. 4  
*Marathonites invariabilis* .....5(3), 206, fig. 5  
*Mariella (Mariella)* .....5(3), 173  
*Mariella (Mariella) aff. circumtaeniata* .....5(3), 175, fig. 11  
*Mariella (Mariella) cenomanensis* .....5(3), 174, fig. 10  
*Martinia sp.* .....5(4), 300, fig. 8  
*Martiniopsis sp.* .....5(4), 300, fig. 8  
*Mawsonia brasiliensis* .....6(4), ?, figs. 1-4  
*Megacricetodon gregarious* .....6(3), 246, fig. 8  
*Megalodon (Megalodon) yanceyi* .....6(1), 70, figs. 3-4  
*Megangulus maximus* .....6(2), 138, fig. 6  
*Megousia sp.* .....5(4), 290, fig. 6  
*Melonis affinis* .....6(2), 155, fig. 11  
*Melonis pompilioides* .....6(2), 155, fig. 11  
*Meristocorpus explicatus* .....6(1), 35, fig. 8  
*Meristocorpus ostentus* .....6(1), 34, fig. 7  
*Mesoturrilites* .....5(3), 171  
*Mesoturrilites aff. corrugatus* .....5(4), 238, fig. 8  
*Mesoturrilites cf. aumalensis* .....5(3), 166, fig. 3  
*Mesoturrilites pombetsensis* .....5(3), 172, figs. 8, 9  
*Metaplex crenulata* .....5(4), 264, figs. 1, 2  
*Metoposaurus diagnosticus* .....6(1), 55, fig. 13  
*Metoposaurus ouazzouri* .....6(1), 55, fig. 13  
*Millardia meltada* .....6(3), 254, fig. 16  
*Miosesarma japonicum* .....5(4), 269, fig. 4  
*Miosesarma naguraense* .....5(4), 269, fig. 4  
*Modiolus maedae* .....5(2), 124, figs. 3-5  
*Monia sp.* .....6(1), 108, fig. 7  
*Munseyella hatatatensis* .....5(4), 248, fig. 6  
*Munseyella hatatatensis* .....6(1), 6, fig. 6  
*Munseyella hatatatensis* .....5(4), 249, fig. 6  
*Munseyella indica* .....6(2), 198, fig. 2  
*Muricidae? gen. and sp. indet.* .....6(2), 136, fig. 5  
*Mus (Pyromys) saxicola* .....6(3), 241, fig. 2  
*Mus flynni* .....6(3), 242, figs. 3, 8  
*Mus musculus* .....6(3), 243, figs. 4, 5  
*Mus musculus tytelri* .....6(3), 241, figs. 2, 6, 7  
*Mus saxicola* .....6(3), 244, fig. 6  
*Myalina (Myalina) cf. wyomingensis* .....6(1), 71, fig. 4

- Mysella*.....5(1), 68, fig. 8  
*Mysella* sp. ....5(1), 67, fig. 7

## N

- Nankinella* sp. ....6(4), ?, fig. 8  
*Nanlingella* cf. *meridionalis*.....6(4), ?, fig. 8  
*Naticidae*? gen. and sp. indet. ....6(2), 136, fig. 5  
*Neocyprideis* *raoi* .....6(2), 198, fig. 2  
*Neomonoceratina paraoertlii* .....6(2), 200, fig. 3  
*Neonesidea oligodentata*.....6(1), 90, fig. 5  
*Neopellucistoma inflatum* .....6(1), 88, fig. 3  
*Neopronorites skvorzovi* .....5(3), 204, fig. 3  
*Neospirifer* cf. *fasciger*.....5(4), 300, fig. 8  
*Neospirifer* sp. ....6(3), 290, fig. 4  
*Neospiriferinae* gen. and sp. indet. ....6(3), 290, fig. 4  
*Nerita* (*Theliostyla*) *albicilla*.....5(1), 22, figs. 1–5  
*Nipponocythere bicarinata*.....6(1), 90, fig. 5  
*Nodosinelloides* sp. ....6(4), ?, fig. 9  
*Nonionella japonica* .....6(2), 155, fig. 11  
*Nordophiceras jacksoni*.....5(3), 208, fig. 7  
*Nucleolina diluta* .....6(2), 202, fig. 4  
*Nucula* sp. ....6(1), 108, fig. 7

## O

- Orbiculoidea* cf. *jangarensis*.....5(4), 290, fig. 6  
*Orbirhynchia* .....5(4), 320  
*Orbirhynchia* aff. *boussensis* .....5(4), 322, fig. 2  
*Orbirhynchia reedensis*.....5(4), 322, fig. 2  
*Oridorsalis umbonatus* .....5(3), 197, fig. 3  
*Oxytoma tetoriense* .....5(2), 125, fig. 4

## P

- Pachyphiloia* sp. ....6(4), ?, fig. 9  
*Paijenborchella* cf. *tsurugasakensis* .....6(1), 10, fig. 7  
*Paijenborchellina indica* .....6(2), 204, fig. 5  
*Paijenborchellini* gen. et sp. indet. ....6(2), 200, fig. 3  
*Pakkokuhyus lahirii* .....6(4), ? fig. 2  
*Palaeofusulina* sp.....6(4), ?, fig. 8  
*Palmenella limicola* .....5(4), 249, fig. 6  
*Palmenella limicola*.....6(1), 10, fig. 7  
*Palmoconcha irizukii*.....6(1), 5, fig. 5  
*Palmoconcha rajui* .....6(2), 202, fig. 4  
*Paracandona andhraensis* .....6(2), 204, fig. 5  
*Paraceltites elegans* .....5(3), 208, fig. 7  
*Paracypris khuialaensis* .....6(2), 204, fig. 5  
*Paracytheridea neolongicaudata* .....5(4), 249, fig. 6  
*Paradoxostomatidae* spp. ....6(1), 90, fig. 5  
*Parakrithella pseudodonta* .....6(1), 88, fig. 3  
*Parapelomys robertsi* .....6(3), 254, fig. 16  
*Parasphenarina cavernicola* .....6(3), 301, figs. 2–12

- Parasphenarina* .....6(3), 301  
*Pattalophyllia* sp.....5(1), 59, fig. 1  
*Pedum spondyloideum*.....5(1), 65, fig. 5  
*Peppersites ellipticus* .....6(1), 32, fig. 6  
*Percnon planissimum* .....5(4), 263, figs. 1, 2  
*Perissocytheridea japonica*.....6(1), 90, fig. 5  
*Perissocytheridea* sp.....6(1), 88, figs. 3, 5  
*Permundaria asiatica* .....5(4), 294, fig. 7  
*Phacosoma chikuzenensis*.....6(1), 108, fig. 7  
*Phlyctocythere japonica* .....6(1), 88, fig. 3  
*Pictothyris picta* .....5(2), 90, fig. 3  
*Pictothyris* sp. ....5(2), 96, figs. 8, 9  
*Pinctada maculata* .....5(1), 35, fig. 2  
*Pitar matsumotoi* .....6(1), 108, fig. 7  
*Placentamina* sp. ....6(2), 158, fig. 7  
*Plagusia dentipes*.....5(4), 263, figs. 1, 2  
*Pleuromya hidensis* .....5(2), 125, fig. 4  
*Plicatipollenites gondwanensis* .....6(1), 34, fig. 7  
*Plicifuscus* cf. *plicatus* .....5(3), 220, fig. 3  
*Popanoceras annae* .....5(3), 206, fig. 5  
*Poronaiia poronaiensis* .....6(2), 162, fig. 9  
*Portlandia* (*Portlandella*) *watasei* .....6(3), 261, fig. 3  
*Potonieisporites brasiliensis* .....6(1), 32, fig. 6  
*Potonieisporites densus* .....6(1), 32, fig. 6  
*Potonieisporites elegans*.....6(1), 32, fig. 6  
*Potonieisporites novicus*.....6(1), 32, fig. 6  
*Potonieisporites ovatus* .....6(1), 32, fig. 6  
*Potonieisporites simplex*.....6(1), 32, fig. 6  
*Potonieisporites* sp.....6(1), 34, fig. 7  
*Potonieisporites triangulatus* .....6(1), 32, fig. 6  
*Praeglobobulimina pyrula* .....6(2), 164, fig. 10  
*Prionocyclus germari*.....5(1), 48, fig. 2  
*Prionocyclus hyatti*.....5(1), 48, fig. 2  
*Prionocyclus macombi* .....5(1), 48, figs. 2, 4  
*Prionocyclus novimexicanus* .....5(1), 48, fig. 2  
*Prionocyclus wyomingensis*.....5(1), 49, fig. 3  
*Pristerodon mackayi* .....5(3), 179, figs. 2–4, 7  
*Procerolagena* sp. cf. *P. gracilima* ....6(2), 164, fig. 10  
*Protocardia* sp.....5(2), 125, fig. 4  
*Protohaploxypinus amplus* .....6(1), 35, fig. 8  
*Protohaploxypinus bharadwajii* .....6(1), 34, figs. 7, 8  
*Protohaploxypinus* sp. cf. *Striatopodocarpites magnificus* .....6(1), 35, fig. 8  
*Pseudoaurila japonica*.....6(1), 90, fig. 5  
*Pseudonodosaria* sp. cf. *P. conica*.....6(2), 164, fig. 10  
*Pseudopolymorphina* sp.....6(2), 164, fig. 10  
*Pseudovidalina* spp. ....6(4), ?, fig. 9  
*Pterelectroma zebra* .....5(1), 63, fig. 4  
*Ptychognathus* sp. aff. *P. ishii*.....5(4), 264, fig. 2  
*Pullenia eocenica* .....6(2), 155, fig. 11  
*Pullenia salisburyi* .....6(2), 155, fig. 11  
*Punctatisporites gretensis* .....6(1), 27, fig. 3  
*Punctatisporites* sp.....6(1), 27, fig. 3



## Q

*Quinqueloculina seminula compacta* ....6(2), 164, fig. 10

## R

*Raistrickia cephalata* .....6(1), 27, figs. 3, 9  
*Raistrickia* sp. cf. *R. saetosa* .....6(1), 27, fig. 3  
*Raphconilia*? sp. ....6(4), ?, fig. 9  
*Rectobolivina asanoi* .....6(2), 224, figs. 4, 10, 13  
*Rectobolivina bifrons* .....6(2), 224, figs. 4, 8, 9, 13  
*Rectobolivina clavata* .....6(2), 224, figs. 4, 10  
*Rectobolivina clavatostriatula* .....6(2), 232, fig. 13  
*Rectobolivina discontinuosa* ....6(2), 224, figs. 4, 10, 13  
*Rectobolivina raphana* .....6(2), 224, figs. 4, 8, 11, 13  
*Rectobolivina striatula* .....6(2), 224, figs. 4, 11  
*Recurvoidella* sp. cf. *R. lamella* .....6(2), 160, fig. 8  
*Recurvoides* sp. ....6(2), 160, fig. 8  
*Reesidites minimus* .....5(4), 234, fig. 4  
*Reichelina changhsingensis* .....6(4), ?, fig. 8  
*Reophax tappuensis* .....6(2), 158, fig. 7  
*Reticulatia* sp. ....5(4), 290, fig. 6  
*Reticulophragmium amakusaensis* .....6(2), 162, fig. 9  
*Rhynchopora* sp. ....5(4), 300, fig. 8  
*Ricinia* sp. ....5(1), 61, fig. 3  
*Robertsonites* cf. *tuberculatus* .....6(1), 14, fig. 8  
*Robertsonites japonicus* .....6(1), 14, fig. 8  
*Robertsonites reticuliformis* .....6(1), 14, fig. 8  
*Robertsonites* sp. ....5(4), 249, fig. 6  
*Robertsonites yatsukanus* .....6(1), 5, figs. 5, 8  
*Robustaurila* spp. ....6(1), 90, fig. 5  
*Rosita fornicata* .....5(4), 280, fig. 4  
*Rosita patelliformis* .....5(4), 280, fig. 4  
*Rotundracythere*? sp. ....5(4), 249, fig. 6  
*Rugosochonetidae* gen. et sp. indet. ....6(3), 290, fig. 4

## S

*Sacella* sp. ....6(1), 108, fig. 7  
*Sanguinolites ishii* .....6(1), 69, fig. 2  
*Schizocythere hatatensis* .....5(4), 249, fig. 6  
*Schizocythere kishinouyei* .....5(4), 249, fig. 6  
*Scintilla* sp. ....5(1), 66, fig. 6  
*Sclerochilus* sp. ....6(1), 90, fig. 5  
*Semicytherura diluta* .....6(2), 204, fig. 5  
*Semicytherura henryhowei* .....5(4), 249, fig. 6  
*Semicytherura* spp. ....6(1), 90, fig. 5  
*Septatoechia* .....5(4), 326  
*Septatoechia* aff. *Rhynchonella baugasii* .5(4), 325, fig. 4  
*Septatoechia amudariensis* .....5(4), 325, fig. 4  
*Septatoechia inflata* .....5(4), 325, fig. 4  
*Septifer (Mytilisepta)* sp. ....6(2), 136, fig. 5  
*Sesarma (Parasesarma) pictum* .....5(4), 264, fig. 2

*Sesarma (Perisesarma) bidens* .....5(4), 263, fig. 1  
*Sesarmops intermedium* .....5(4), 263, figs. 1, 2  
*Shimodaia pterygiota* .....5(2), 90, figs. 3, 8, 9  
*Siamotherium pondaungensis* .....6(4), ? fig. 2  
*Sigmoidella pacifica* .....6(2), 164, fig. 10  
*Siphogenerina striatula* .....6(2), 232, fig. 13  
*Skolithos* isp. ....5(2), 127, fig. 6  
*Solemya suprajurensis* .....5(2), 125, fig. 4  
*Spelaeotrilites* .....6(1), 33  
*Spelaeotrilites arenaceus* .....6(1), 30, fig. 5  
*Spelaeotrilites triangulus* .....6(1), 30, fig. 5  
*Spinileberis furuyaensis* .....6(1), 90, fig. 5  
*Spinileberis pulchra* .....6(1), 90, fig. 5  
*Spinileberis quadriaculeata* .....6(1), 88, fig. 3  
*Spinileberis* sp. ....5(4), 249, fig. 6  
*Spiriferella keilhavii* .....6(3), 290, fig. 4  
*Spiriferella lita* .....5(4), 300, fig. 8  
*Spiriferella persaranae* .....6(3), 290, fig. 4  
*Spirileberis* sp. ....5(4), 248, fig. 6  
*Spirophycus* isp. ....5(2), 127, fig. 6  
*Stefaniniella colosii* .....5(1), 59, fig. 1  
*Stenoscisma margaritovi* .....5(4), 300, fig. 8  
*Striatoabieites* sp. cf. *S. anaverrucosus* ....6(1), 35, fig. 8  
*Striatopodocarpites* sp. ....6(1), 35, fig. 8  
*Striatopodocarpites* sp. cf. *S. phaleratus* ..6(1), 34, fig. 7  
*Striatosporites heyleri* .....6(1), 30, fig. 5  
*Striomonosaccites ovatus* .....6(1), 34, figs. 7, 9  
*Subbotina* sp. ....6(2), 168, fig. 12  
*Subprinocyclus minimus* .....5(2), 104, fig. 3  
*Subprinocyclus neptuni* .....5(2), 105, fig. 6  
*Subprinocyclus minimus* .....5(2), 103, fig. 2

## T

*Taeniaesporites* sp. ....6(1), 35, fig. 8  
*Tapes*? sp. ....6(2), 138, fig. 6  
*Terebratalia coreanica* .....5(2), 90, figs. 3, 8, 9  
*Tetorimya carinata* .....5(2), 124, figs. 3-5  
*Thalassoceras gemmellaroi* .....5(3), 207, fig. 6  
*Thracia shokawensis* .....5(2), 125, fig. 4  
*Trachyleberis ishizakii* .....6(1), 92, fig. 7  
*Trachyleberis scabrocuneata* .....6(1), 88, fig. 3  
*Trachyleberis* sp. ....5(4), 247, fig. 5  
*Transennatia gratiosa* .....5(4), 290, fig. 6  
*Treptoceras yokoyamai* .....6(1), 123, fig. 1  
*Trochammia* sp. cf. *T. asagaiensis* ....6(2), 164, fig. 10  
*Trominina hokkaidoensis* .....6(3), 261, fig. 3  
*Turrilites* .....5(3), 163  
*Turrilites acutus* .....5(3), 166, figs. 3, 5, 6  
*Turrilites* aff. *costatus* .....5(3), 166, fig. 3  
*Turrilites complexus* .....5(3), 164, figs. 1-4  
*Turrilites costatus* .....5(3), 166, figs. 3, 4  
*Turrilites mikoku* .....5(3), 170, fig. 7

*Turrilites scheuchzerianus* .....5(3), 166, figs. 3, 4  
*Turritella* sp. ....6(3), 261, fig. 3

## U

*Uraloceras* sp. ....5(3), 206, fig. 5  
*Urocythereis pohangensis* .....6(1), 10, fig. 7  
*Uroleberis rasilis* .....6(2), 204, fig. 5  
*Urushtenoidea crenulata* .....5(4), 294, fig. 7

## V

*Vallatisporites russoi* .....6(1), 30, fig. 5  
*Vallatisporites* sp. ....6(1), 30, fig. 5  
*Vellatisporites arcuatus* .....6(1), 30, fig. 5  
*Venericardia subnipponica* ....6(1), 107, figs. 6, 7, 9, 10  
*Verrucosisorites andersonii* .....6(1), 30, fig. 5  
*Verrucosisorites* sp. cf. *V. morulatus* ....6(1), 27, fig. 3  
*Vervilleina* sp. ....6(4), ?, fig. 9

*Vidrioceras* sp. ....5(1), 15, figs. 1-3  
*Vulsella vulsella* .....5(1), 59, fig. 1

## W

*Waagenoconcha* cf. *imperfecta* .....5(4), 294, fig. 7  
*Waagenoconcha permocarbonica* .....5(4), 294, fig. 7

## X

*Xestoleberis opalescenta* .....6(1), 88, fig. 3  
*Xestoleberis* spp. ....6(1), 90, fig. 5  
*Xestoleberis subglobosa* .....6(2), 204, fig. 5

## Y

*Yakovlevia kaluzinensis* .....5(4), 290, fig. 6  
*Yezocythere gorokuensis* .....5(4), 247, fig. 5  
*Yoldia* sp. ....6(1), 108, fig. 7



## CONTENTS

## Vol. 5 No. 1 (April 30, 2001)

	Page	Figures
Takao Ubukata: Morphological approaches in paleobiology .....	1	
Enrico Savazzi: Morphodynamics of an endolithic vermetid gastropod .....	3-11	1-6
Kazushige Tanabe, Cyprian Kulicki, Neil H. Landman and Royal H. Mapes: External features of embryonic and early postembryonic shells of a Carboniferous goniatite <i>Vidrioceras</i> from Kansas ....	13-19	1-3
Takenori Sasaki: Macro- and microstructure of shell and operculum in two Recent gastropod species, <i>Nerita</i> ( <i>Theliostyla</i> ) <i>albicilla</i> and <i>Cinnalepeta pulchella</i> (Neritopsina: Neritoidea) .....	21-31	1-7
Takao Ubukata: Geometric pattern and growth rate of prismatic shell structures in Bivalvia .....	33-44	1-9
Richard A. Reymont and W. James Kennedy: Evolution in morphometric traits in North American Collignoniceratinae (Ammonoidea, Cephalopoda) .....	45-54	1-7
Enrico Savazzi: A review of symbiosis in the Bivalvia, with special attention to macrosymbiosis ....	55-73	1-9
Erratum: Article by Takashi Hasegawa and Takayuki Hatsugai in Vol. 4, Nos. 2 and 4 .....	75	

## Vol. 5 No. 2 (June, 29, 2001)

Mohamed Zakhera, Ahmed Kassab and Kiyotaka Chinzei: <i>Hyotissocameleo</i> , a new Cretaceous oyster subgenus and its shell microstructure, from Wadi Tarfa, Eastern Desert of Egypt .....	77-86	1-7
Michiko Saito and Kazuyoshi Endo: Molecular phylogeny and morphological evolution of laqueoid brachiopods .....	87-100	1-9
Fumihisa Kawabe and Yasunari Shigeta: The genus <i>Hourcquia</i> (Ammonoidea, Pseudotissotiidae) from the Upper Cretaceous of Hokkaido, Japan: biostratigraphic and biogeographic implications .....	101-109	1-11
Masayuki Ehiro: Some additional Wuchiapingian (Late Permian) ammonoids from the Southern Kitakami Massif, Northeast Japan .....	111-114	1-2
Shuji Niko: Middle Carboniferous orthoconic cephalopods from the Omi Limestone Group, Central Japan .....	115-120	1-2
Toshifumi Komatsu, Ryo Saito and Franz T. Fürsich: Mode of occurrence and composition of bivalves of the Middle Jurassic Mitarai Formation, Tetori Group, Japan .....	121-129	1-7
Noritoshi Suzuki and Kazuhiro Sugiyama: Regular axopodial activity of <i>Diplosphaera hexagonalis</i> Haeckel (spheroidal spumellarian, Radiolaria) .....	131-140	1-5
PROCEEDINGS .....	141-142	

## Vol. 5 No. 3 (September 28, 2001)

Keiichi Hayashi: Ostracode biostratigraphy of the Lower Cretaceous Wakino Subgroup in northern Kyushu, Japan .....	143-162	1-12
Tatsuro Matsumoto and Takemi Takahashi: Further notes on the turrilitid ammonoids from Hokkaido-Part 2 (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-XC) .....	163-176	1-11
Sanghamitra Ray: Small Permian dicynodonts from India .....	177-191	1-12
Ritsuo Nomura: Quantification of optically granular texture of benthic foraminiferal walls .....	193-200	1-7
Yasunari Shigeta, Yuri D. Zakharov and Royal H. Mapes: Origin of the Ceratitida (Ammonoidea) inferred from the early internal shell features .....	201-213	1-7
Kazutaka Amano and Mikiko Watanabe: Taxonomy and distribution of Plio-Pleistocene <i>Buccinum</i> (Gastropoda: Buccinidae) in northeast Japan .....	215-226	1-5
PROCEEDINGS .....	227-228	

## Vol. 5 No. 4 (December 31, 2001)

Tatsuro Matsumoto and Takemi Takahashi: A study of <i>Hypoturrilites</i> (Ammonoidea) from Hokkaido (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-XCI) .....	229-240	1-8
Tatsuhiko Yamaguchi and Hiroki Hayashi: Late Miocene ostracodes from the Kubota Formation, Higashi-Tanagura Group, Northeast Japan, and their implications for bottom environments ....	241-257	1-10
Hiroaki Karasawa and Hisayoshi Kato: The systematic status of the genus <i>Miosesarma</i> Karasawa, 1989 with a phylogenetic analysis within the family Grapsidae and a review of fossil records (Crustacea: Decapoda: Brachyura) .....	259-275	1-4
Kazuyoshi Moriya, Hiroshi Nishi and Kazushige Tanabe: Age calibration of megafossil biochronology based on Early Campanian planktonic foraminifera from Hokkaido, Japan .....	277-282	1-4
Jun-ichi Tazawa: Middle Permian brachiopods from the Moribu area, Hida Gaiken Belt, central Japan	283-310	1-8
Kazushige Tanabe, Royal H. Mapes and David L. Kidder: A phosphatized cephalopod mouthpart from the Upper Pennsylvanian of Oklahoma, U.S.A. ....	311-318	1-5
Neda Motchurova-Dekova: Taxonomic and phylogenetic aspects of the shell ultrastructure of nine Cretaceous rhynchonellide brachiopod genera .....	319-330	1-5
<b>PROCEEDINGS</b> .....	331-332	

## Vol. 6 No. 1 (April 30, 2002)

Gengo Tanaka, Koji Seto, Takao Mukuda and Yusuke Nakano: Middle Miocene ostracods from the Fujina Formation, Shimane Prefecture, Southwest Japan and their paleoenvironmental significance .....	1-22	1-9
Rodolfo Dino and Geoffrey Playford: Stratigraphic and palaeoenvironmental significance of a Pennsylvanian (Upper Carboniferous) palynoflora from the Piauí Formation, Parnaíba Basin, north-eastern Brazil .....	23-40	1-9
Dhurjati Prasad Sengupta: Indian metoposaurid amphibians revised .....	41-65	1-18
Keiji Nakazawa: Permian bivalves from the H. S. Lee Formation, Malaysia.....	67-72	1-4
Yutaro Suzuki: Systematic position and palaeoecology of a cavity-dwelling trilobite, <i>Ityophorus undulatus</i> Warburg, 1925, from the Upper Ordovician Boda Limestone, Sweden .....	73-83	1-5
Moriaki Yasuhara, Toshiaki Irizuki, Shusaku, Yoshikawa and Futoshi Nanayama: Changes in Holocene ostracode faunas and depositional environments in the Kitan Strait, southwestern Japan .....	85-99	1-8
Norihiko Sakakura: Taphonomy of the bivalve assemblages in the upper part of the Paleogene Ashiya Group, southwestern Japan .....	101-120	1-12
<b>SHORT NOTES</b>		
Shuji Niko: Revision of an Ordovician cephalopod <i>Ormoceras yokoyamai</i> (Kobayashi, 1927).....	121-124	1
<b>PROCEEDINGS</b> .....	125-126	

## Vol. 6 No. 2 (June 28, 2002)

Takashi Matsubara: Molluscan fauna of the "Miocene" Maéjima Formation in Maéjima Island, Okayama Prefecture, southwest Japan .....	127-145	1-6
Satoshi Hanagata: Eocene shallow marine foraminifera from subsurface sections in the Yufutsu-Umaoi district, Hokkaido, Japan .....	147-178	1-12
Toshiyuki Kimura: Feeding strategy of an Early Miocene cetothere from the Toyama and Akeyo Formations, central Japan .....	179-189	1-7
Subhash Chandar Khosla and Madan Lal Nagori: Ostracodes from the Intertrappean beds (Early Paleocene) of the east coast of India.....	191-210	1-5
Hisayoshi Kato: Fossil crabs (Crustacea: Decapoda: Brachyura) from the latest Miocene Senhata Formation, Boso Peninsula, Japan .....	211-217	1-5



- Shungo Kawagata and Akio Hatta: Internal test morphology of the genus *Rectobolivina* (Cushman, 1927) from the Late Cenozoic Miyazaki Group, southwestern Japan ..... 219-236 1-15

**PROCEEDINGS** ..... 237-238

Vol. 6 No. 3 (September 30, 2002)

- Rajeev Patnaik: Enamel microstructure of some fossil and extant murid rodents of India ..... 239-258 1-18
- Yutaka Honda: Paleobiogeographic significance of *Trominina hokkaidoensis* (Hayasaka and Uozumi) (Gastropoda: Buccinidae) from the basal part of the Tanami Formation (Oligocene) of the Kii Peninsula, southern Japan ..... 259-263 1-3
- Gengo Tanaka and Noriyuki Ikeya: Migration and speciation of the *Loxoconcha japonica* species group (Ostracoda) in East Asia ..... 265-284 1-14
- Guang R. Shi, Shuzhong Shen and Jun-ichi Tazawa: Middle Permian (Guadalupian) brachiopods from the Xiujiminqi area, Inner Mongolia, north-east China, and their palaeobiogeographical and palaeogeographical significance ..... 285-297 1-4
- Neda Motchurova-Dekova, Michiko Saito and Kazuyoshi Endo: The Recent rhynchonellide brachiopod *Parasphenarina cavernicola* gen. et sp. nov. from the submarine caves of Okinawa, Japan .... 299-319 1-14
- Artém M. Prokofiev: First finding of an articulated actinopterygian skeleton from the Upper Devonian of Siberia and a reappraisal of the family Moythomasiidae Kazantseva, 1971 (Osteichthyes) .... 321-327 1-2
- Errata: Article by Takashi Matsubara in Vol. 6, No. 2 ..... 329

**PROCEEDINGS** ..... 330

Vol. 6 No. 4 (December 31, 2002)

- Fumio Kobayashi: Lithology and foraminiferal fauna of allochthonous limestones (Changhsingian) in the upper part of the Toyoma Formation in the South Kitakami Belt, Northeast Japan ..... 331-342 1-9
- Yoshikata Yabumoto: A new coelacanth from the Early Cretaceous of Brazil (Sarcopterygii, Actinistia) ..... 343-350 1-4
- Shuji Niko: *Echigoceras sasakii*, a new Middle Carboniferous nautilid from the Omi Limestone Group, Central Japan ..... 351-355 1-4
- Tatsuro Matsumoto: Turrilitid ammonoid *Carthaginites* from Hokkaido (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-XCIV) ..... 357-361 1-2
- Takehisa Tsubamoto, Masanaru Takai, Naoko Egi, Nobuo Shigehara, Soe Thura Tun, Aye Ko Aung, Aung Naing Soe and Tin Thein: The Anthracotheriidae (Mammalia; Artiodactyla) from the Eocene Pondaung Formation (Myanmar) and comments on some other anthracotheres from the Eocene of Asia ..... 363-384 1-10
- Shuji Niko and Masayuki Ehiro: Permian orthoconic cephalopods of the Ochiai Formation in the Southern Kitakami Mountains, Northeast Japan ..... 385-389 1-4

**PROCEEDINGS** ..... 391-392

**INDEX OF GENERA AND SPECIES** ..... 394-403





## 行事予定

◎第152回例会は、2003年1月24日（金）～26日（日）に横浜国立大学教育人間科学部にて開催します。1月24日（金）にシンポジウムとして「白亜紀海洋無酸素事件の解明：世話人 平野弘道・北里 洋・西 弘嗣」が、また1月25日（土）にシンポジウム「中・古生代微化石研究の現状と将来－テレーン解析後の使命－：世話人 指田勝男」が開催されます。なお、講演の申し込み締め切りは、2002年11月29日（金）です。講演申し込みの予稿集原稿送付の際には発表で使用する機器（液晶プロジェクター、OHP、スライドなど）の希望について明記して下さい。

◎2003年年会総会は、2003年6月27日（金）～29日（日）に静岡大学理学部で開催の予定です。シンポジウム「生物多様性を古生物学から考える：世話人 塚越 哲・北村晃寿・生形貴男」を開催予定です。講演の申し込み締め切りは2003年5月2日（金）の予定です。このほか、夜間小集会などの希望予定がありましたら、2002年12月初旬までに行事係までお知らせ下さい。

### 個人講演・シンポジウム案の申し込み方法

個人講演の申し込みは予稿原稿を下記まで直接お送り下さい。E-mail やファックスでの申し込みは原則として受け付けておりません。また行事全般に関するお問い合わせも行事係か行事係幹事までお寄せください。

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Vol. 6, No. 4

December 31, 2002

### CONTENTS

#### ARTICLES

- Fumio Kobayashi:** Lithology and foraminiferal fauna of allochthonous limestones (Changhsingian) in the upper part of the Toyoma Formation in the South Kitakami Belt, Northeast Japan ..... 331
- Yoshitaka Yabumoto:** A new coelacanth from the Early Cretaceous of Brazil (Sarcopterygii, Actinistia) ..... 343
- Shuji Niko:** *Echigoceras sasakii*, a new Middle Carboniferous nautilid from the Omi Limestone Group, Central Japan ..... 351
- Tatsuro Matsumoto:** Turrilitid ammonoid *Carthaginites* from Hokkaido (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin—XCIV) ..... 357
- Takehisa Tsubamoto, Masanaru Takai, Naoko Egi, Nobuo Shigehara, Soe Thura Tun, Aye Ko Aung, Aung Naing Soe and Tin Thein:** The Anthracotheriidae (Mammalia; Artiodactyla) from the Eocene Pondaung Formation (Myanmar) and comments on some other anthracotheres from the Eocene of Asia ..... 363

#### SHORT NOTES

- Shuji Niko and Masayuki Ehiro:** Permian orthoconic cephalopods of the Ochiai Formation in the Southern Kitakami Mountains, Northeast Japan ..... 385

#### PROCEEDINGS ..... 391

#### List of reviewers ..... 393

#### INDEX OF GENERA AND SPECIES ..... 394













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